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CONTENTS.

PAGE

No. 1. The Ascidians Collected by the United States Fisheries Bureau Steamer Albatross on the Coast of California during the Summer of 1904, by Wm. E. Ritter. With Plates 1-3 1-52

Introduction 1

Table of Species 1-2

Description of Genera and Species 3-44

Bibliography 45-46

Explanation of Plates 48-52

No. 2. Behavior of the Starfish *Asterias forreri* de Loriol, by H. S. Jennings. With 19 text-figures 53-185

Introductory 56

Behavior of the Starfish 58

Respiration and its protection by the Pedicellariae 59-63

Detailed Behavior of the Pedicellariae 64-82

Capture of Food 84-94

Behavior of the Starfish in selecting the Conditions of Existence 94-101

Reaction to Light 102-110

Positive Reactions 113-118

Righting Reaction 120-147

Formation of Habits in the Starfish 148-169

Unified Impulse and the Determination of the varied Activities under its Influence 169-182

Concluding Statement 183

Bibliography 184

No. 3. The Early Life-History of *Dolichoglossus pusillus* Ritter, by B. M. Davis. With plates 4-8 187-226

Introduction 188

Periods of Development 190-191

Early Habits and Activities of *D. pusillus* 192-195

Early Growth Stages 200-212

Occurrence of Half Embryos and Double Embryos 213

Comparison of *D. pusillus* and *Amphioxus* with reference to Origin of Body Cavities 213

Bibliography 216

Explanation of Plates 218-226

PAGE

No. 4. Notes on two Amphipods of the Genus *Corophium* from the Pacific Coast, by J. Chester Bradley. With plates 9-13 227-252
Introduction 227
Key to the Species of *Corophium* 229
Description of Genera and Species 229-230
Comparison of the Species 239-241
Bibliography 242
Explanation of Plates 244-252

No. 5. The Incrusting Chilostomatous Bryozoa of the West Coast of North America, by Alice Robertson. With Plates 14-24 253-344
Introduction 253
Description of Genera and Species 255-315
Bibliography 316-321
Explanation of the Plates 324-344

No. 6. Exuviation, Autotomy and Regeneration in *Ceratium*, by Charles Atwood Kofoid. With 33 text-figures 345-386
Introduction 346
Ecdysis 347-348
Exuviation 349-359
Normal Autotomy in *Ceratium* 360-374
Regeneration in *Ceratium* 377-383
Bibliography 385

No. 7. Notes on Some Obscure Species of *Ceratium*, by Charles Atwood Kofoid 387-393
Introduction 387
Description of Genera and Species 388-391
Bibliography 392-393

Index .....

UNIVERSITY OF CALIFORNIA PUBLICATIONS
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THE ASCIDIANS COLLECTED BY THE UNITED STATES FISHERIES BUREAU STEAMER *ALBATROSS* ON THE COAST OF CALIFORNIA DURING THE SUMMER OF 1904

BY

WM. E. RITTER

BERKELEY
THE UNIVERSITY PRESS

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THE ASCIDIANS COLLECTED BY THE UNITED STATES FISHERIES BUREAU STEAMER *ALBATROSS* ON THE COAST OF CALIFORNIA DURING THE SUMMER OF 1904*

BY

WM. E. RITTER.

The work of the Albatross from March 1 to June 11, 1904, furnished material for the only bit of information we have concerning the off-shore ascidians of the California region. No shore collections are included in this report. It should be stated, however, that many of the dredging stations, probably more than half, and particularly those in and about Monterey Bay, were in depths of only a few fathoms—100 or less.

The following systematic table of the fourteen species in the collection shows the depths and also the geographic position with reference to Point Conception, from which the species come. Full data as to habitat, so far as the field records furnish them, are given under each species.

Family Molgulidae—	DEPTH.	LOCALITY.
Halomolgula n. gen.		
1. Halomolgula ovoidia n. sp.	1000 fath.	South of Point Conception.
2. Molgula regularis n. sp.	71-67 fath.	South of Point Conception.

* This paper is published with the permission of Honorable G. M. Bowers, United States Commissioner of Fish and Fisheries.

Family Cynthiidae—

3. Halocynthia okai n. sp.	10-80 fath.	North of Point Conception.
4. Boltenia echinata n. sp.	21-48 fath.	North of Point Conception.
5. Culeolus pyramidalis n. sp.	2259 fath.	South of Point Conception.
6. Microcosmus transversus n. sp.	33 fath.	South of Point Conception.
7. Styela milleri n. sp.	2228 fath.	South of Point Conception.
8. Styela gibbsii Stimp.	40 fath.	North of Point Conception.

Family Ascidiidae—

Benthascidia n. gen.

9. Benthascidia michaelseni n. sp.	2182 fath.	South of Point Conception.
10. Ascidia clementea n. sp.	654-111 fath.	South of Point Conception.
11. Ciona mollis n. sp.	1100 fath.	South of Point Conception.

Family Distomidae—

12. Cystodites cretaceous v. Dr.	43-111 fath.	North of Point Conception.

Family Polyclinidae—

13. Psammaplidium spauldingi n. sp.	33 fath.	South of Point Conception.

Family Didemnidae—

14. Didemnum opacum n. sp.	33 fath.	South of Point Conception.

For about 50 miles to the north of Point Conception, or more exactly Point Arguello, the California coast runs almost due north and south, then for about 70 miles south of the Point the course is nearly east and west. The broad, mountainous triangle thus standing out from the general northwest and southeast trend of the coast constitutes apparently as important a geographical barrier for the littoral life of the coast as do the Tehachapi Mountains, of which it is really a part, for the life of the land.

It will be seen that ten of the fourteen species were taken south of the Point. This seeming greater wealth of off-shore species southward is the more striking when it is considered that the stations occupied on each side of the Point were practically the same, there having been 133 to the south and 130 to the north.

Some interesting results are revealed by an examination of the bathymetric distribution of the species. The following table presents the facts:

1. Depth, 2000 fathoms or more; number of stations, 7; number of species, 3.

2. Depth, 2000 to 1000 fathoms; number of stations, 9; number of species, 3.

3. Depth, 100 to 500 fathoms, 41; number of stations, 41; number of species, 0.

4. Depth, 500 to 1 fathoms; number of stations, 206; number of species, 8.

This gives—Depth 1: 1 species to 2 1-3 stations.
Depth 2: 1 species to 3 stations.
Depth 3: 0 species to 41 stations.
Depth 4: 1 species to 25 1-4 stations.

Of the 263 stations occupied only 16 produced ascidians. Two of these, namely, 4420 and 4425, produced two species each; 4420 was in a depth of 33 fathoms and 4425 in 1100 fathoms, both in the vicinity of San Nicolas Island and both on sandy or muddy bottom. Only three species were taken at more than one station, *Halocynthia okai* coming from five stations, all in the Monterey district, in less than 100 fathoms.

The data are too few to permit of much in the way of generalization, but indications in two directions are rather strong. In the first place, the off-shore ascidian fauna is considerably richer south than north of Point Conception, so far as concerns the areas worked over at this time; and, second, that the deep water along and just beyond the continental shelf is more prolific of this form of animal life than is the shallower in-shore water.

Genus HALOMOLGULA.

Test beset with processes each containing *calcareous spicules*. Branchial membrane with nine folds on each side. Infundibula present, large. Branchial stigmata small, irregular in form and distribution, rarely with any curvature. One gonad on each side of the body, the left in the intestinal loop.

Halomolgula ovoida, n. sp.

Pl. 1, figs. 1 to 6.

Superficial Characters.—Form varying from almost perfectly spherical to strongly depressed biscuit-shape with elliptical base. Outline in general very regular and even; surface, except on area

of attachment, wholly free from foreign substances. *Siphons* projecting scarcely at all above the general surface. Attached usually by posterior end, the area of attachment being usually broad and often extended by a flange, more or less regular, of test. *Color* light grey; in some regions, especially about the anterior end, approaching white. *Size*, longest diameter of largest specimens, 4 cm.; short diameter of same specimen, 3.5 cm.; more usual size, longer diameter about 2 cm., shorter about 1.5 cm. *Test* thin and papery, entire surface beset with minute stellate tubercles, each of which contains several short, rod-like *calcareous spicules* (pl. 1, figs. 1, 2 and 3). Except for presence of the opaque white tubercles just mentioned, test quite transparent.

Mantle.—Delicate, easily separating from the test, its muscle bands delicate though numerous, especially in the anterior half of the animal, where they are disposed both meridianally and circularly, with also some fibres running obliquely.

Branchial Apparatus.—Siphons very short or wholly absent. Branchial orifice appearing on the surface usually as a longitudinal slit. Branchial orifice probably with six lobes. *Branchial tentacles* from twelve to fourteen, compound, rather large, with several intervening ones much smaller (pl. 1, fig. 4). *Hypophysis* mouth simple, elliptical, situated slightly to the right side and far removed from the tentacular circlet. *Peripharyngeal* groove distant from the tentacular circlet and pursuing a meandering course by bending in between the anterior ends of the branchial folds, fig. 5.

Ganglion—Extremely long and narrow, extending from in front of the hypophysis backward behind it to a distance three or four times the length of the latter. *Dorsal lamina* a broad, heavy, crenulated membrane beset with numerous conical processes. *Branchial sac*, with nine folds on each side, eight of which are large, the one on each side of the endostyle being small. Internal longitudinal vessels on each side of each fold varying from six on the smaller folds to nine or ten on the larger. *Infundibula* large, quadrilateral, frequently notched at their inner borders, *i.e.*, the borders toward the inner margins of the folds. *Stigmata* small and irregularly distributed, usually short elliptical, but in some regions somewhat curved. Those of the infundibula gener-

ally smaller than those between the folds. *Transverse vessels* limited to the folds, and to the intervals between the infundibula, pl. 1, figs. 5 and 6.

Intestinal Tract.—Wide, simple open loop situated across the posterior dorsal side of the animal, somewhat to the left. Stomach not large, sharply set off from the esophagus but not from the intestine, the wall irregularly folded. Anus bordered by five or six petaloid lobes. *Renal organs* in the form of two or three distinct patches on the inner surface of the mantel in the vicinity of the gonads, the largest patch being lateral to the right gonad. *Gonads* one on each side of the body, the left in the intestinal loop, each long and sausage-shaped.

The dull white, clean-surfaced, egg-shaped habitus of this fine species gives an assemblage of the animals a striking appearance. The coreaceous consistency of the test causes the specimens to keep their form to an unusual degree, in spite of the action of preserving fluids. Nearly all of the hundred and fifty individuals examined were attached to a net-like hexactinellid sponge, and considerable expanses of the sponge are still adhering to the specimens. The minute, close-set, rigid spicule-bearing processes of the test give the surface considerably the nature of the chagrin of some sharks. Examination of the processes with a hand lens discovers them to be arranged about the orifices in quite regular fashion (pl. 1, fig. 2). In perspective the processes are regularly goblet-shaped, with the mouth of the goblet taking the form of the Greek acanthus. Each secondary process, corresponding to the petal of the acanthus flower, contains a rod-like calcareous spicule, the distal end of which is pointed, and corresponds to the tip of the process. The spicules do not occur in interior parts of the animal, excepting on the inner surface of the siphons and over a small, well-defined area on the inside of the branchial and atrial chambers, immediately around the orifices. These areas in all probability mark the inturned portion of the ectoderm. After the spicules are destroyed with acid a considerable cluster of cells is observable in the tubercles containing them. These probably produce the spicules. The question of the lobulation of the orifices in this species is unusually difficult. Pl. 1, fig. 2, shows the branchial orifice as seen in a surface view in a specimen with

far more suggestions of lobes than can be recognized in the majority of the large number of individuals examined. There can be no doubt about the presence of six lobes here. Whether they stand for realities in the living animal, or are merely results of retraction, I am not quite sure, but assume the former. The condition of the atrial orifice is still more dubious. Usually in an ascidian, where the lobes can not be made out by surface examination, separation of the test from the mantle brings out the true state of things. Applying this method here does not help. Indeed the edge of the orifice, when thus freed, is even more lobeless than when viewed from the surface.

As will have been noticed from the diagnosis the branchial sac is peculiar in several respects. The quadrilateral outline of the infundibula is unusual in Molgulids. Frequently the infundibula in this species are quite as broad at the inner end as at the outer, and the notching or forking of many of them is quite a new feature. The branchial folds, excepting the one nearest the endostyle on each side, are broad and thin, and as a consequence the infundibula are unusually flattened. The two folds adjacent to the endostyle are so thin as to be easily overlooked. The small size and irregularity of the stigmata is another peculiarity. One may examine the whole area of a branchial membrane without noticing more than the slightest inclination to curvature among the orifices. In other individuals a pronounced tendency of this sort is seen, some of the stigmata being curved to a quarter or even a half circle. Again, the membrane itself is unusually thick and heavy in the infundibula, and generally the stigmata are here considerably smaller than in other parts of the sac.

What I interpret as the "renal organs" are rather insignificant as compared with these structures in many other Molgulids. As mentioned in the diagnosis, they are situated on the inner surface of the mantle in the vicinity of the gonads. The largest one observed, in a large specimen, was not more than 2 mm. across. It consisted of a peculiar meandered folding of the epithelial layer of the mantle, the cells of which, though somewhat larger than those of the adjacent parts, had seemingly little in common with the tissue characteristic of the renal organ of the Molgulidae. But little coloring matter has been observed in any of these structures in this species, and no vesicles have been seen.

The gonads are practically of the same size on the two sides of the body. Only in the larger individuals are they fully developed. In these the axial part of the sausage-shaped mass is readily seen to be the ovary, and here many of the ova are relatively large. Along this ovarian axis, for its entire length, the pear-shaped testis lobes are disposed on both sides. These lobes are uniform in size and shape, and are placed with their larger ends directed away from the axis. Both gonads converge toward the atrial chamber so that their orifices, as well as the esophageal opening and the anus are near together, and all are near the atrial siphon.

The character, which more than any other, has compelled me to establish a new genus for this species is the calcareous spicules in the test. Starting from this feature, and considering along with it the slight extent to which the stigmata are curved, I have tried to force the species into the genus *Rhabdocynthia*, Herdman. But even relying on the spicules alone, the fact that in our present species they are confined to the test, whereas in *Rhabdocynthia* they are present in other tissues, as the mantel, branchial vessels, etc., makes a quite sharp contrast between the two types. There is, however, an undoubted tendency toward a curvature of the stigmata in *H. ovoidia*. When this is coupled with the well-marked infundibula of the branchial sac it becomes obvious that *Rhabdocynthia* will not receive our species, indeed that it must be associated with the Molgulas rather than with the Cynthias.

After the spicules the characters most seriously in the way of assigning the species to any recognized genus are the two orifices, the number of branchial folds, the position of the gonad of the left side, and probably the structure of the renal organ.

No Molgulid, so far as I am aware, possesses more than seven branchial folds on each side. Since, however, the genus Molgula is allowed six and seven folds (and five if, as Hartmeyer '03 believes, *Pera* should not be separated off), I should not be disposed to permit even the nine folds of *H. ovoidia* to stand in the way of assigning it to an old genus were there no other difficulties in the way.

As regards the relation of the intestinal tract and gonads. *H. ovoidia* has greater resemblance apparently to *Eugyra molgul-*

oides (Sluiter '04) than to any other species. But of course the characters of the dorsal lamina and branchial membrane put *Eugyra* out of consideration for our species.

Finally turning to the troublesome orifices, the recently established *Astropera* (Pizon '98), possessing as it does a gonad on each side of the body, holds out at first sight some promise of furnishing a lodging place for our species. But the absence of the peculiar petaloid lobes of *Astropera*, taken with differences in the number of branchial folds, and in the position of the left gonad relative to the intestine, to say nothing of the absence of the spicules in *Astropera*, make it out of the question to seriously consider uniting our species to Pizon's genus.

I conclude, then, that *Halomolgula ovoidia* is a representative of a group of Molgulids that holds some such relation to *Molgula* as that held by *Rhabdocynthia* to *Cynthia*. When, however, one searches through the known species of the family Molgulidae for a species that might have been the parent of *H. ovoidia*, not much success is met with.

In view of the fact, noted by Sluiter '04, that the species of *Rhabdocynthia* are, most of them, inhabitants of seas in which coral reefs abound, it is worth while to point out that such is not the case with *H. ovoidia*. There are very few corals or other calcium carbonate-producing species in the region to which this animal belongs. The collection contains about one hundred and fifty specimens.

Station 4425, 21.8 miles S. 7°E. point of San Nicholas Island, 1000 to 1100 fathoms, bottom green mud and fine sand, and globigerina, associated with much hexactinelid sponge. April 13, 1904.

Molgula regularis, n. sp.

Pl. 1, figs. 7 and 8.

Superficial Characters.—Ellipsoid, very regular in outline, surface entirely covered with foraminiferous shells and sand particles, which cling closely to the great number of filiform processes of the test. No definite area of attachment, though a thin membrane-like substance loosely adhering to one side of some of the specimens may mark the place of contact with the substratum on

which the body rests. No siphon nor orifices visible without removing the covering of foreign particles. Length of longest specimen, 4 cm.; thickness of same, 2.3 cm. Other specimens of the collection but little smaller.

Test.—Thin and leathery after adhering particles are removed; semi-transparent. Filamentous processes very numerous and slender, but little branched, foreign particles clinging to them throughout their length.

Mantle.—No definite muscle bands excepting around the orifices. Here large and strong bands regularly disposed radially around the orifices, uniform in length and terminating abruptly at their distal ends; also a narrow zone of circular fibres around each orifice. The rest of the mantle containing an open meshwork of fine fibres (pl. 1, fig. 7).

Branchial Apparatus.—Siphons entirely wanting. Orifices not far apart, the branchial being well forward, the atrial near the middle of the length of the body. On removal from the test the orifices found to be slightly but unequivocally six-lobed (branchial), and four-lobed (atrial). Branchial *tentacles* about ten, of several sizes, the largest large and copiously branched. *Hypophysis-mouth* a narrow ellipse directed somewhat obliquely to the long axis of the animal. *Peripharyngeal band* running close to the anterior ends of the branchial folds. *Ganglion* a little more than twice as long as broad, less than its length behind the hypophyseal mouth. *Dorsal lamina* a plain-edged rather broad membrane (pl. 1, fig. 8). *Branchial sac* with six prominent folds. Longitudinal vessels of the folds delicate and rather irregular in number and course; about five on each side of each fold, nearly equally spaced from one another. *Infundibula large*, extending full size to the edge of the folds and leaving little space between them along the transverse vessels. *Stigmata* large everywhere; little curved except as they extend around the infundibula.

Intestinal Tract.—Situated on the left side at the extreme posterior end of the animal; loop a close one. *Stomach* not large, nearly twice as long as broad, smooth-walled. *Intestine* very long and thin, of uniform diameter throughout; rectal half forming a wide semi-circle; anus without lobes. *Renal organ* consisting of a large brown, regular elongate central portion, surrounded by a

still larger clear part; situated on the right side of the body, close to the posterior end of the endostyle. *Gonads,* one on each side of the body, that on the left in front of the intestinal loop (pl. 1, fig. 7).

This species, clear-cut in its generic characters and also sharply set off from any other species of the genus, needs little of comment beyond what is brought out by the diagnosis. While it is one of those species so welcome to the systematist because of the positiveness in both its generic traits and in its specific differentiation from other known Molgulas, it is at the same time a good example of those species which present such a combination of specific characters as to make the question of what its closest affinities within the genus are, so difficult, but at the same time so interesting. For example, as regards surface covering, form, hypophysis mouth, number of folds in the branchial sac, and position of left gonad, *M. regularis* has much in common with *M. tenax* Traustedt, and on the whole one may conclude that it is more closely related to this than to any other species. At the same time, as regards the mantel muscles, the form of the gonads and the structure of the so-called liver, the two differ sharply. *M. tenax* has no such development and disposition of mantle muscles about the siphons as *M. regularis* presents us with (pl. 1, fig. 7). The testis of *tenax,* as shown by Hartmeyer '03, is a rounded single mass on each side instead of a whole series of small elongate lobes as in our species; and is situated to one side of the ovary instead of being scattered round it so as to give the latter a central position with reference to it. The liver in *tenax* is, according to Hartmeyer, "very exceptional in its enormous development." Nothing of this sort is found in *M. regularis.* But *M. arctica* Kiaer is a species in which the mantle musculature is very similar to that of *M. regularis.* Likewise the structure and relation of the male and female gonads in this far northern species are much like those of *M. regularis.* In the latter the relatively great elongation of the combined male and female glands, with the testes divided up into distinct and quite widely separated lobes, these being deployed around the ovary and scattered along its whole length, is to be regarded as an extreme expression of the same type as that represented by the glands of *M. arctica.* In this latter species, however,

we seem to have about the opposite extreme of the type, namely, variation in the direction of shortening the axis and concomitant crowding together of the testis lobes. Again, *M. arctica* would appear to conform to the usual Molgula type as regards the liver. But *M. arctica* has seven folds in the branchial sac, and, according to Kiaer, a narrow anus "with a faint indication of four lobes on the margin." Whether, consequently, *M. regularis* shall be regarded as more closely related to *tenax* or *arctica* will depend on the ever-recurring question of the value to be placed on different characters. There appears to be no particular prospect of reaching a generally recognized standard of reference for the question.

The collection contained half a dozen specimens. Station 4309, Point Loma Light N.44°, E. 8.6°, March 3, 1904, 67-73 fathoms, bottom fine sand and shells.

Halocynthia okai, n. sp.

Pl. 1, figs. 9 to 16.

Superficial Characters.—Nearly spherical, though some specimens distinctly elongated antero-posteriorly. Attached by posterior end, area of attachment usually small. Except on area of attachment, *thickly covered with long straight spines*, these bearing numerous small secondary spines. Each spine bearing a *radial tuft* of from four to six or eight spinelets at its tip. In addition to the long spines, numerous sessile whorled spinelets on the test between the bases of the large spines (pl. 1, figs. 9, 11, 12 and 13). *Siphons* short and often so hidden by spines as to be found with difficulty. *Color* brown to light gray. *Length* of largest specimens, 80 mm.; thickness of same, 55 mm. *Length* of spines of full-grown individuals, 10 mm. and more. *Test* strong and leathery, rarely more than 1 or 1.5 mm. thick. *Mantle* rather thick, not separating readily from the test; mantle musculature consisting of evenly-spaced bands radiating from each siphon, the crossing of the two series giving the mantle the appearance of closely woven cloth. The muscles extending over the entire body, but somewhat weaker in the intestinal regions.

Branchial Apparatus.—Siphons very short and broad, the branchial somewhat larger. Both four-lobed, the lobes distinct and tumid. *Tentacles* about sixteen in number, large and much branched, the branches arranged rather constantly in pairs of nearly uniform size, and bearing numerous secondary and tertiary branchlets (pl. 1, fig. 14). *Hypophysis* mouth horseshoe-shaped, somewhat broader than long, the ends turned in but not produced into spirals, the two horns of equal length. *Dorsal lanquets short*, slender and numerous. *Branchial* membrane with ten large folds on the left side and nine on the right, with suggestion of an additional fold on each side next to the endostyle. Each of the largest folds with ten prominent longitudinal vessels on each side, making twenty in all (pl. 1, fig. 16). Transverse vessels distinctly of two sizes. *Stigmata* small, uniform in size, extending lengthwise with reference to the folds. *Endostyle*, large and tortorous. *Ganglion* long and narrow, in some specimens extending nearly the entire distance between the two siphons.

Digestive Tract.—Situated on the left side, the loop about one and one-half times as long as broad, the rectal bend short; stomach small, not clearly set off from the intestine; anus with a distinct rim.

Gonads.—Consisting of about five cylindrical masses on the left side and four on the right, those of the left within the intestinal loop.

In the collection are a number of young specimens that are no larger than the largest specimens of *H. villosa* that I have seen, yet the spines are nearly as long and closely crowded in these as in the largest individuals. In no case are they scattered as they are in *villosa*. This species adds another to the considerable number of spiny Cynthias. It belongs to the *hilgendorfi* section of this group of species, *i. e.*, to the section having the branchial stigmata extending lengthwise with reference to the branchial folds instead of crosswise, as they do in *H. echinata* and its congeners. Oka (1906) has recently described two other species from the coast of Japan which in all probability belong to the same group, though the important point of the position of the stigmata he does not mention. Oka's species are *H. owstoni* and *H. ritteri*. *H. okai* appears to resemble *H. owstoni* more closely than any of the other

species, but from this it differs in the absence of the spirally inrolled horns of the hypophysis mouth; in the less number of tentacles, *owstoni* having thirty; and in the larger number of longitudinal vessels on the branchial folds, *owstoni* having seventeen or eighteen of these.

As our information now stands, the distribution of these Cynthias presents an interesting problem. There can be no doubt, as it appears, that *H. hilgendorfi* Traustedt, *H. owstoni* Oka, *H. ritteri* Oka, of Japan, and *H. okai*, of the Pacific Coast of the United States, are very close of kin. Furthermore, *H. echinata* L., *H. arctica* Hartmr., *H. villosa* Stimp., and probably *H. castanciformis* v. Dr., constitute another group of closely related forms that is, however, sharply separated from the *hilgendorfi* group by the difference in the stigmata already indicated. The *echinata* group seems to be well represented in the Arctic regions, the Bering Sea and Alaskan waters, but thus far is unknown south of Puget Sound on the American coast (*H. villosa* Stimp, Herdman 1898, Ritter 1901), or south of northern Japan (*H. arctica* Hartmeyer 1906). On the other hand, none of the *hilgendorfi* group are yet known from the region intervening between northern Japan and northwestern United States. (On re-examining certain specimens from Puget Sound which I (Ritter 1901) formerly assigned to *H. villosa*, I now find to be undoubtedly the same as those from the coast of Southern California which I am naming *H. okai*). In other words, the *hilgendorfi* group seems to be replaced at the north on both east and west shores of the Pacific by the rather distinct *echinata* group. Of course farther collecting may bring to light members of the *hilgendorfi* group in the Bering Sea and other Alaskan waters. It is desirable that a closer study, both as to structure and as to distribution, should be made of all these forms.

About twenty-five specimens were taken from five stations, as follows: 4552 Point Pinos light, S. 73°E., 4 miles, June 9, 1904, 73 fathoms, green mud and rocks; 4554 Point Pinos light, S. 76°E., 3 miles, June 9, 1904, 60 to 80 fathoms, green mud and rocks; 4555 (practically same as 4554); 4557 Point Pinos light, S. 25° W., 3.1 miles, June 9, 1904, 53 fathoms, rock bottoms.

Boltenia echinata, n. sp.

Pl. 2, figs. 17 to 19.

Superficial Characters.—Body ovate to elongate, surface beset with simple, slender, sharp, rather remote spines. Siphons distinct or not, at nearly opposite ends of body. Peduncle slender, of nearly uniform diameter throughout, slightly thicker at junction with the body; attached to dorsal side somewhat nearer the branchial orifice, starting off at a sharp angle with the long axis of the body. *Color* brownish white, body and peduncle nearly the same. Greatest length of body 1.75 cm. to 2 cm., greatest thickness 1 cm. to 1.5 cm. Length of peduncle two to three times that of body, greatest thickness of peduncle not more than 4 mm.

Test, very thin but firm and parchment-like, of uniform thickness, semi-transparent; entire body spiny, the spines of several lengths, slender, sharp, usually unbranched, but an occasional long one with one or more secondary processes. Each spine situated on a raised, clearly delimited area of test, the larger ones on larger areas, the smaller on smaller areas. No spines on proximal half of peduncle.

Mantle, very thin and closely adherent to the test, musculature consisting of a set of small, moderately numerous, regularly arranged and evenly spaced radial and circular bands, the radials of both orifices distinctly stronger than the circulars; and in addition a felt-work of much finer fibres.

Branchial Apparatus.—Siphons so short as to be unrecognizable in preserved specimens, or but little projecting from the surface of body, both regularly four-lobed. *Tentacles* about twenty, of unequal sizes, the largest long and copiously branched, the few strong primary branches carrying a great number of secondary branches. *Hypophyseal mouth* simple horse-shoe shaped, about as long as broad. *Branchial membrane* with twelve folds of very unequal size; internal longitudinal vessels, five or six on each face of the largest folds with one or two between the folds, small and all nearly of same size. *Stigmata* directed *transversely* to the longitudinal vessels, in general regularly elongate but in some regions shorter and with long

axes in various directions (pl. 2, fig. 18). *Dorsal languets* rather long, close together, no membrane.

Digestive Tract.—Situated on left side of body, loop regular, rather wide; stomach not large nor clearly set off from intestine; a short pedunculate pouch with shallow lobulated surface projecting from ventral edge of the stomach. *Gonads* two, one on each side of body, the left within the intestinal loop, both elongate and tortuous. The *ovary* constituting the main axial portion of each mass; the *testis* consisting of a double row of somewhat lighter colored elevations, along the outer side of each ovary.

There are two specimens of this species in the collection; one (fig. 17) from station 4558 Point Pinos Light, S. 79°, W. 2 miles, June 9, 1904, 40 to 48 fathoms, rock bottom; the other from station 4303 (fig. 18), Point Loma Light, N. 12°, W. 6.1 miles, March 1, 1904, 21 fathoms, gray sand bottom.

Cursory comparison of figs. 17 and 19 suggests that the two are quite different animals. This conjecture gains strength when it is noted that the first station mentioned is near Monterey and the other near San Diego. The diagnosis is given almost wholly from the specimens shown in figs. 17 and 19. I am inclined to believe the two to be distinct species; nevertheless the differences between them are not sufficiently great nor of a kind to warrant the separation on the strength of the single specimen of each available for examination. Although differences exist in some of the internal features as well as in their superficial ones, these differences are still more of a kind that may well be supposed to be individual. Should it in the future be found necessary to separate them, *Boltenia echinata* would be the name of the Monterey form, and a new name would have to be given the San Diego one.

Attention may be called to the apparently branched condition of the peduncle of the San Diego specimen. This probably comes from the peduncles of several individuals having fused together during growth, as the parts are now inseparable.

The transverse direction of the branchial stigmata is an especially noteworthy characteristic of the species. This recalls the same peculiarity in the *echinata* group of Halocynthias referred to under *H. okai* of this paper. Of the other Boltenias that pos-

sess the same character, *B. elegans* Herdman, has more in common with *B. echinata* than has any other species, but *elegans* is wholly devoid of surface spines. *B. bouvetensis* Michaelsen (Michaelsen, 1904) is interesting in this connection as furnishing a sort of intermediate condition between longitudinal and transverse stigmata. According to Michaelsen the stigmata in this species are very irregular, some being long, some short, some curved, some longitudinal, and some transverse.

Culeolus pyramidalis, n. sp.

Pl. 2, figs. 20 and 21.

Superficial Characters.—Body rather regularly pyramidal, slightly compressed, peduncle attached at apex of the pyramid close to the branchial orifice and on its ventral side, fig. 20. Base of the pyramid marked by the atrial orifice dorsally, the papillary band laterally, and by a pronounced patch of longer test papillae ventrally. Outline of base elliptical with long axes of ellipse dorso-ventral; base strongly convex, fig. 21. Siphons none. Surface in general even, but a series of not well defined grooves radiating from the atrial orifice. Entire surface thickly beset with minute papillae, and a distinct, sinuous *papillary band* marking off the base of the pyramid. Peduncle very long and slender, of nearly uniform diameter throughout, terminating in a disc provided with strong holdfasts. *Color* of body yellowish gray; peduncle blue gray. Greatest length of body 2.5 cm., long axis of elliptical base 2 cm., short axis of same 1.5 cm. Length of peduncle 19 cm.

Test thin, scarcely 1 mm. thick, firm and leathery, bearing a great number of low, conical papillae, each of which is situated in a definite area of clear test; blood ampullae in the test substance, and extending into the longer test papillae of the band.

Mantle thin and transparent except for the muscle bands, which are, especially on the atrial portion of the body, rather strong though not close together, the circular and longitudinal running at nearly a right angle to one another, producing a large-meshed network.

Branchial Apparatus.—No siphons nor lobes for either orifice,

branchial orifice close to the insertion of the peduncle and dorsal to this, much smaller than atrial, slightly elliptical, elongate crosswise of body, with a low but definite and even lip. Atrial orifice very large and wide open, distinctly elliptical, elongation crosswise of the body, the ventral border somewhat more arched than the dorsal; edge of the test bordering the opening so even as to give the impression that the orifice has been cut with a die. *Tentacles* of unequal sizes very long and strong, but branches neither numerous nor large. *Branchial membrane* without stigmata, composed of very loose wide-meshed netting of blood vessels, the whole so crumpled and distorted in specimens available as to make the true structure impossible of determination. A few spicules, mostly unbranched, in branchial vessels; more spicules, these irregularly branched, in tentacles. *None of the spicules calcareous*, they giving no evolution of gas when treated with acids.

Digestive Tract.—On left side, stomach not clearly set off from intestine, thin walled, and not (?) provided with coeca. Intestinal loop simple, narrow, irregular, the two limbs close together, the rectal being ventral to the stomach and running nearly parallel with and close to the endostyle for some distance. *Gonads* not determined.

There is not sufficient material in the collection to enable me to adequately describe this species. Enough can, however, be made out to warrant the conclusion that it is unidentifiable with any *Culeolus* hitherto described. The external characters, upon which I have chiefly to rely, which appear to differentiate the species, are: the position of the papillary band with reference to the atrial orifice. In most other species possessing the band it is continuous around the orifice instead of, as here, being interrupted by it (pl. 2, fig. 21). *C. quadrula* Sluiter 1904 approximates *C. pyramidalis* in this particular more closely, perhaps, than does any other species, but *quadrula* appears to be without the tuft of larger papillae at the lateral ends of the atrial opening, and the especially prominent patch at the ventro-posterior angle or prominence of the body. Furthermore the surface of the test of *pyramidalis* is not laid off into any such quadrangular areas as is that of *quadrula*. The radiating plicae and shallow

grooves around the atrial opening appear to be without a counterpart in any other species (fig. 21). It might be conjectured that these are artifacts. Their regularity, however, and particularly the sharpness of the grooves preclude, I believe, the possibility of their being accounted for in this way when the firmness of the test is considered. There is little doubt that they are structural. Again *C. pyramidalis* seems to outdo all other species in the great size and wide-openness of its atrial orifice.

The one character of internal structure that seems to be unique is the spicules. In other species these are spoken of as being calcareous. If they are actually of this nature in all other cases, then *pyramidalis* stands alone in possessing spicules of some other substance. What they are I do not know, but they are unaffected by hydrochloric acid.

There are three specimens of *Culeolus* in the collection, from two stations, *viz.*, 4394 and 4396, only a few miles apart. I am not sure that all belong to the same species. Two of the specimens, much smaller than the one here figured and described, have some important peculiarities of their own. One has a saeculated stomach wall and in this particular resembles *C. murrayi* Herdman and *C. thysonatus* Sluiter. The number of specimens is not sufficient to enable me to decide what the significance of these diversities may be. I consequently prefer to leave the matter for the present without an attempt to more definitely assign the smaller individuals to their species. Since the animals come from a great depth, over 2,000 fathoms, the question here raised is of special interest, and it is greatly to be hoped that more material may be secured before long.

Station 4394, 32° 54′ N., 121° 15′ W. (just at the foot of the continental slope west of San Diego), March 30, 1904, 2,259 fathoms, soft gray mud. Station 4396, 33° 01′ N., 121° 32′ W., March 31, 1904, 2,228 fathoms, red mud.

Microcosmus transversus, n. sp.

Pl. 2, figs. 22 and 23.

Superficial Characters.—Cylindrical, axis transverse making the orifices at nearly opposite ends; attached by less than middle half of ventral side, the branchial end turning up somewhat more

than the atrial, and considerably narrower at the end, making an ill-defined branchial siphon. Surface very uniform and entirely free of foreign bodies. *Color* milk-white, uniform throughout. *Test* semi-cartilaginous, opaque, from one to two or more mm. thick; from its inner surface a filmy, half gelatinous, irregularly areolated layer readily separates. *Mantle* rather thick and heavy, its musculature consisting of especially large, regular, slightly separated muscle bands, the circular bands being largest. Both mantle proper and its muscles much reduced on the ventral side making the viscera, the gonads in particular, distinctly visible through the mantle.

Branchial Apparatus.—Branchial orifice distinctly four-lobed, atrial situated at the large posterior end of the cylindrical body, making a siphon scarcely recognizable. The test duplicature turned into the branchial siphon of considerable thickness and remaining with the test when the latter is removed from the animal. *Tentacles* unequal in size, sparsely and irregularly branched, few in number, about ten or twelve. *Peripharyngeal* band strong, very close to the tentacular circle. *Hypophysis* horse-shoe shaped, longer than broad, opening turned outward for about one-fourth of a circle; horns not spirally coiled but bent slightly inward. Dorsal lamina a broad area scarcely projecting into the branchial chamber though its two edges are raised into slight folds. *Branchial membrane* with six folds on each side, the second to fourth inclusive very large; about five or six longitudinal vessels on each face of each of the prominent folds. *Stigmata* rather narrow, regular, longitudinal.

Digestive Tract.—Intestinal loop long, narrow, simple, situated on left side of body, both esophagus and anus near the atrial siphon, and the axis of the loop placed nearly parallel to the endostyle. *Esophagus* short and narrow, forming nearly a semicircle. *Stomach* but little thicker than intestine and not clearly set off from latter (less so than figure indicates). Wall with many inconspicuous longitudinal folds. A peculiar bulb-like inflation in the rectum near the anus.

Gonads two, one on each side, the left within the intestinal loop. *Ovary* cylindrical, regular, constituting an axial part, around which the uniformly sized, crowded *testis* lobes are dis-

posed. Right gonad close to the endostyle and extending parallel with it.

A single specimen from station 4420, east point of San Nicolas Island, S. 77°, W. 5.7 miles, April 12, 1904, 33 fathoms, bottom fine gray sand.

Judging from certain other species of simple ascidians that present considerable variability in the distance apart of the orifices, we may suppose that acquaintance with more specimens of *M. transversus* will find the unusual form of this particular individual not to be wholly constant for the species. We may be quite sure, however, that an exceptionally wide separation of the siphons is characteristic of the species.

As to general form *M. transversus* is approached in the remoteness of its siphons by *M. arenaceous* Sluiter (Sluiter 1904), but this latter species lacks considerable of being so nearly a cylinder with orifices at opposite ends, as is the particular specimen of *M. transversus* under observation. Furthermore *M. arenaceous* has a thin leathery test bearing numerous processes, and is covered more or less completely with sand. *M. transversus* is peculiarly smooth surfaced and free from sand. When note is taken of the fact that the animal comes from a sandy bottom, this trait as distinguishing it from *M. arenaceous* becomes of special weight. Another equally important distinction between the two species is found in the hypophysis mouth. This in *M. arenaceous* is broken up into a number of wholly distinct parts.

On the whole *M. transversus* appears to be a specially well defined species. It should be said, however, that in a few particulars of internal structure a more careful examination of more specimens may somewhat modify the diagnosis. For example, I am considerably in doubt about the number of tentacles. It is not impossible that a minute branchial fold may be present on each side next to the endostyle. The dorsal lamina should also receive more study. Again attention ought to be called to the fact that the stomach is not in reality so positively folded as fig. 23 gives the impression that it is. The folds are very small and may be easily overlooked.

Styela milleri, n. sp.

Superficial Characters.—Cylindric-ovoid, attached by a small area at posterior end; orifices both branchial the atrial somewhat toward the dorsal side. No siphons, but orifices distinct, both regularly four-lobed. Surface broken by a few irregular low wrinkles anteriorly, by large patches of indurated or warty thickenings posteriorly; the area of attachment bearing many short filamentous processes. *Color* yellowish brown, the warty areas darker. Length 22 cm., thickness 1.2 cm. *Test* very thin but parchment-like, readily detachable from the mantle; dull white on inner surface. *Mantle* thin, muscle fibers uniformly distributed, longitudinal and circular, not disposed in definite bands, the longitudinal generally somewhat stronger.

Branchial Apparatus.—Siphons entirely wanting, both orifices with clear-cut lobes. *Tentacles* of several lengths, about thirty long and slender ones of nearly equal length, and probably as many more shorter, but of unequal lengths. *Dorsal tubercle* prominent, bearing the broad simple horse-shoe shaped *hypophysis mouth*. *Branchial membrane* with four folds on each side, all broad except the one next the endostyle on the right side, two of the folds on each side next the endostyle drawn out anteriorly into long processes. Internal *longitudinal* vessels numerous and large, the largest folds having eighteen or twenty on each face. *Transverse* vessels consisting of a series of large and strong ones of nearly but not quite equal size, and between many of these, others very delicate, usually crossing the stigmata. *Stigmata* long and slender, with the intervening vessels also very narrow. *Dorsal lamina* a broad thin membrane not thin nor toothed, but closely crimped. *Endostyle* heavy, irregularly tortuous throughout.

Intestinal Tract.—On the left side of the animal. *Stomach* regular, elongate-melon shaped, the wall thrown into numerous close, regular ridges or folds. A short duodenal section of the intestine bent closely back upon the stomach, and from this a much longer rectal section having at about the middle of its length a short flexure extending forward along the dorsal side of the body almost to the atrial orifice.

Gonads.—Ovaries consisting of a single, much elongated cylindrical mass on each side, extending from antero-dorsal to postero-ventral. *Testes* consisting of closely crowded nodular masses grouped around the posterior ends of the ovaries.

Although this species is a typical Styela quite devoid of striking specific characters, I still find it impossible to assign it to any hitherto described species. On the whole it seems to have more in common with a Straits of Magellan form described by Michaelsen, and regarded by him as a variety of *S. canopus* (Sav.), which he names *magalhaensis*, than with any other known form. This variety, however, usually has distinct siphons, and two ovaries on each side, though according to Michaelsen, 1900, the siphons are occasionally wanting, and in a few instances but a single ovary on each side is present. Were both these variations to occur in the same specimen, the resemblance to our species would be close indeed. However, it seems that the long free ends of the branchial folds in *S. milleri* are without a counterpart in *S. canopus* var. *magalhaensis*. Probably also the test of this latter form is thicker and more uneven than it is in *S. milleri*.

It is interesting to note that this Styela shares with other deep-sea species the trait of possessing nothing distinctive of its remarkable habitat as contrasted with shallow water or even littoral species of the genus. Going upon the testimony of *Culeolus* in particular, but of other deep-sea genera as well, the generalization might be reached that deep-sea life causes degeneration of the branchial membrane. The abyssal Styelas exhibit no evidence of such effects. In the present species, for example, the membrane is if anything rather stronger than usual. It might be conjectured, I suppose, that these particular deep-sea species have not been subjected to this unusual environment long enough to produce the change. But what is the evidence of their being new arrivals in the great depths? There are now eight species, namely, *bathybia* Bonnevie, *bythia* Herd., *flava* Herd., *pusilla* Herd., *squamosa* Herd., *glans* Herd., *oblonga* Herd., and *milleri* Ritter, known from great depths, and it seems as though some of them should show the beginning of reduction of the sac if it is true that an effect of this sort is an inevitable

consequence of such an environment. This does not always seem to be the case. In fact the sacs of two of the species coming from the greatest depths of all are if anything rather stronger than the average. Concerning *S. bythia*, which was dredged by the Challenger in 2,600 fathoms, Herdman remarks that the branchial sac "looks rather thick and opaque," and that this is due to the "large number of internal longitudinal bars present," Herdman '82, p. 152. The sac of *S. milleri* may likewise be said to be rather thick and opaque for a Styela, and from the same circumstance.

A single specimen, station 4396, Long. 33° 01′ N., Lat. 121° 32′ W., March 31, 1904, 2,228 fathoms, bottom red mud.

Styela gibbsii Stimp.

Two specimens of this species were obtained at station 4558, and four at station 4431. The largest of these is 16 mm. long, and all the others, excepting one which is obviously young, are but little smaller. Since these come from two localities and are so nearly uniform in size they may be taken as fully grown. The average length of a hundred or more specimens from Puget Sound, now before me, is 35 or 40 mm., these likewise being quite uniform in size.

As the species has not been found in Alaskan waters, nor in any abundance on the Southern California coast, it is justifiable to assume that Puget Sound is near its metropolis, and that Southern California is near the southern limit of its range. At Puget Sound it lives in abundance on shore rocks above low-water mark.

Station 4431, Brockway Point, Santa Rosa Island, S. 43° W., 5.2 miles, April 15, 1904, 41 fathoms, yellow mud bottom. Station 4558, Point Lobos Light, S. 79° W., 2 miles, June 9, 1904, 40 fathoms, rock bottom.

Benthascidia, n. gen.

Long pedunculate; no siphons and no lobes to the apertures; the branchial orifice very large and not closable. Tentacles simple, short, very numerous, and many short papillae on the inner surface of the intratentacular circlet. Branchial membrane very delicate and *without true stigmata.*

Benthascidia michaelseni, n. sp.

Pl. 2, figs. 24 to 30.

The two specimens secured were both too much mutilated to permit clear recognition of what the general form of the body was. Unfortunately too a number of important anatomical points could not be made out with certainty. The description must consequently be understood to be incomplete. The specimens were curiously broken in almost exactly the same way.

External Characters.—Long pedunculate, the peduncle being smooth and column-like, thickest at base, gradually diminishing in diameter for about a third of its entire length, then as gradually increasing again to pass insensibly into the body (pl. 2, fig. 24). Length of the peduncle to where body thickening begins about 220 mm. Base of peduncle rising abruptly from a mass of fine short roots, or hold-fasts by which the animal was undoubtedly anchored to the bottom. Thickness of the peduncle immediately above the roots about 30 mm.

Form of the body undetermined, but quite certainly no projecting siphons. Whole animal, both body and peduncle hyaline to transparent, without pigment, the visceral mass showing through distinctly. Test for the most part very thin and soft, though thickened to 3 or 4 mm. on portions of the body, this thickening not uniform but producing low nodulations in nearly circular areas of sizes varying from a few mm. to 15 or 20 mm.

Mantle very thin and delicate, separating readily from the test. Muscle fibers of the mantle arranged in delicate though definite bands running generally in the same direction, hence parallel with one another (fig. 26). These considerably stronger and closer together in some portions of the animal than others, though distribution of the heavier portions not determined.

Branchial Apparatus.—Branchial orifice (without siphon) very large, 35 mm. in diameter, circular and without lobes or markings of any sort so far as ascertained. Atrial orifice not found (apparently far remote from the branchial orifice). Branchial *tentacles* minute and very numerous, three or four hundred, simple but irregular in shape, many larger at the free end and somewhat flattened. A great number of minute pro-

cesses projecting from the inner surface of the tentacular area (fig. 29). *Branchial Sac* exceedingly delicate, so much so as to be found with considerable difficulty in the mutilated specimens. No stigmata present but the sac composed of an irregular network of delicate vessels all in the same plane, through which at intervals run larger vessels of more regular course, *p.v.* (pl. 2, fig. 30). The direction of these large vessels with reference to the sac as a whole not determined since no part of the sac in situ has been seen. From the larger vessels other vessels of considerable size and length pass off to the mantle, *b.m.v.* No folds or internal papillae present.

Digestive Tract.—As a whole consisting of a single loop, the esophageal opening and anus being near together (pl. 2, fig. 29). Length of entire loop 5 cm., width of loop in broadest part 4 cm. Esophagus rather thick, more than half as long as stomach. *Stomach* somewhat cask shaped though slightly curved, about two-thirds as broad as long; wall thrown into a large number of fine folds running lengthwise of the organ, those most pronounced at the anterior end where the wall is of a brownish color. Intestine from stomach on diminishing slightly and uniformly in diameter to the anus which is somewhat inconspicuously four-lobed.

Reproductive Organs.—Male and female, situated alongside of and within the intestinal loop. The *ovary* a large curved sac, containing ova of about 2 mm. in diameter,—giant size for tunicate eggs. *Testes* irregular band shape, situated within the loop of the ovary and somewhat beneath it (pl. 2, fig. 27). Sperm duct consisting of half a dozen or more vasa efferentia, as they might be called, running together at a common center. From this center the sperm duct proper arises and takes a nearly direct course parallel with the rectal portion of the intestine, but extending some distance beyond the anus. The sperm duct pronouncedly club-shaped, the narrow end being proximal. (Probable that the expansion of the distal part pertains only to the period of sexual activity.)

I am considerably puzzled over my inability to find a second, presumably atrial orifice. In view of the dilapidated condition of the specimens it would be unwarranted to suppose the creature

possesses but a single orifice. Nevertheless, unless the size of the body is enormous, no considerable portion of the test can be actually lacking, and it is surprising, to say the least, that the same orifice should have been lost in both specimens. A large expanse of test surrounds the orifice present, the branchial in each case, and this it is that leads to the conclusion that the two orifices are widely separated. If this be true, there would be a distinct similarity here between the present species and *Corynascidia*.

The structure of the peduncle deserves more attention than it gets in the diagnosis. I have labeled the core (pl. 2, fig. 24) *b.c.*, "body portion of the column." This I do not from evidence furnished by its structure, that it is an extension of the body wall. I have failed to discover either epithelium or muscle fibers anywhere in the column. The whole core is a firm, gelatinous, transparent material with spherical cells scattered uniformly, but by no means numerously, through it. My chief reason for supposing it to be in reality a portion of the body is that it is from this that the roots, or hold-fasts take their origin (see figure). Assuming these structures to be essentially the same as the hold-fasts occurring in other rooted ascidians, *e.g.*, *Rhizomolgula* and *Octacnemus*, the mantle must have been implicated in their production. There is no lumen, nor yet an axial strand of any sort discoverable in the core.

The outer sheath, fig. 24 *tst.*, is with little doubt entirely testicular. Its matrix does not differ perceptibly from that of the body, but it contains a far greater number and variety of cells than does the body test. Many of these cells are spherical, but many are long and narrow, almost to the extent of deserving to be called fibrous. These extend in all directions and are without regular arrangement.

One might expect to find stiffening or supporting elements of some sort in a stalk of the length of this, but none such exist so far as I have observed. It may perhaps be supposed that the organ serves as an anchor chain rather than as a supporting column.

The test of the body is noteworthy for its extreme transparency and the spareness of the cells contained in it. It is so

transparent that fragments, even after having been in preserving fluids for many months, can be seen in a glass of water only with considerable difficulty. I do not recall having examined the test of any other ascidian in which so few cells are present. Furthermore their regularity of form and size is exceptional. They present almost none of the elongations, stellations, and other irregularities common in most ascidians.

In addition to the general statement about the course of the muscle bundles of the mantle, it should be mentioned that in limited areas, probably though not certainly, in the vicinity of the orifices, bundles at right angles or nearly so, to those already described, are present.

In the diagnosis I have neglected to mention the tuft of tentacles situated within the branchial sac between the esophageal and anal orifices (pl. 2, fig. 28). My reason for this was my doubt about the nature of the organs. The most probable suggestion that can be made is that they are dorsal languets. Their closely grouped condition, their restriction to the small area near the esophageal orifice, and their slenderness, make, however, their interpretation by no means certain. But a still greater difficulty in the way of the suggestion is their position *between* the esophageal and anal appertures. Assuming them to be dorsal languets would involve the supposition that the median dorsal line of the animal passes between these orifices. This assumption I make on the evidence furnished by Corynascidia in this particular. I recognize, however, that the evidence is far from sufficient to establish finally the truth of such an assumption. In the one known species of Coryanascidia, *C. Suhmi* Herdman, the "esophagus opens," according to Herdman's description, "on the dorsal edge," and the rectum "runs anteriorly in close contact with the stomach and intestine." Thus the dorsal line in this species is near enough to the two orifices to warrant the assumption I have made. The tentacles are not only very slender but they are also very thin walled and delicate.

Of the several other remarkable features about this ascidian, I may next speak of the dorsal tubercle and hypothesis. Pl. 2, fig. 29, shows the region where these structures seem quite certainly to have been situated. As a matter of fact, however, I

have been unable to find anything that can be identified as these parts. A peculiar knot, with no definiteness of organization, was present at the apex of the cone-shaped muscular body shown in the figure with its apex truncated. This was connected by tattered portions of tissue with the branchial membrane; but I have tried in vain to find anything in it that I could call gland, nerve ganglion, or duct. I must therefore leave the question of these parts almost as vague as that of the endostyle. The difference is that I have not even found where the endostyle *ought to be.*

The muscle bands in the figure are considerably stronger here than elsewhere in the vicinity, and I have not been able to trace the circular ones entirely around the circle of which they appear to be a segment. As little have I been able to follow out the entire course of the circular groove, *g.i.f.*, beyond the tentacles shown in the figure. No doubt can be entertained, however, that this is a piece of the peripharyngeal band. It is laid off as the figure shows into quite regular nodes by radiating cross grooves. Whether these exist in nature or not, I do not know, but am inclined to believe they do. The complete circle of tentacles I have not been able to find, the total number being calculated from the segment of the circle present. The great number of minute processes on the inner surface within the pharyngeal area, seen in the figure, *p.i.f.*, will not escape the notice of the reader, nor will they fail to excite curiosity as to their significance. I know of nothing comparable to them in any other ascidian.

I have spoken of the branchial sac as being without stigmata, but as consisting of a network of delicate vessels. The criteria applied in affirming that the irregular network of vessels constituting the branchial sac (pl. 2, fig. 30) contains no true stigmata, are two. First, the absence of cilia which are held to be characteristic of all true stigmata in Ascidians; and second, the absence of vessels situated on the inner surface of the web. This last criterion would be valid only on the assumption that the web should really be of the type presented by the genera related to *Corynascidia*, namely, *Hypobythius*, *Abyssascidia*, *Corella*, etc.; that is, that the vascular network present represents the "internal vessels" of the genera mentioned, the true stigmatic membrane being unrepresented in the present species. The possi-

bility, however, that we have to do here with a membrane of the Clavelina type, should not be forgotten, namely, one in which the true membrane is without *internal vessels*. Were this the truth the cilia criterion would be the only one by which the identification could be made. The view that cilia are absent may, I think, be accepted with confidence since were they present there should be no difficulty in observing them, for the specimens were preserved in formalin while still in a fresh condition. It can hardly be supposed that they were lost by post-mortem changes.

Not knowing the orientation of the visceral mass within the animal, I have said nothing in the diagnosis about the direction of the major vessels of the branchial network. From the fragment figured as connected with the visceral mass (pl. 2, fig. 28) it is seen that they run lengthwise of the intestinal loop. As the network is bound to the mantle of the vessels, there is no doubt that the fragment is in its natural position as regards the intestine. It would follow, if my assumption be true that the intrabranchial tentacles are dorsal languets, that these major branchial vessels run lengthwise of the body.

The irregularity in both size and shape of the meshes is most unusual. In this particular the species in hand appears to resemble *Bathypera splendens* Michaelson, more than any other ascidian. This species, however, Michaelson regards, seemingly with full justification, as related to *Molgula*. In other respects there is little in common between our species and *Bathypera*.

The problem of the affinities of this species would be difficult even were our information about its adult structure not so imperfect. That on the whole it has more in common with *Corynascidia* than with any other known genus may be gathered from the descriptions and discussions already presented. The several genera which it resembles to some extent are *Abyssascidia*, *Agnesia*, *Bathypera*, *Bathynoncus*, *Clavelina*, *Corynascidia*, *Eupera*, and *Hypobythius*. The following tabulation of characters of these genera will display most conveniently how *Benthascidia michaelseni* stands with reference to each genus:

	Abyssascidia	*Agnesia*	*Bathypera*	*Bathyoncus*	*Clavelina*	*Corynascidia*	*Eupera*	*Hypotythius*	*Benthascidia*
General form	not pedunculate	not pedunculate	not pedunculate	not pedunculate	elongate, colony formed by budding	pedunculate	pedunculate	pedunculate	pedunculate
Test	soft and transparent	cartilaginous, transparent	leathery with calcarious spicules	Leathery, slightly or not at all transparent	cartilaginous transparent	cartilaginous semi-transparent	cartilaginous transparent	membranous transparent	cartilaginous transparent
Appertures	lobed	inconspicuously lobed	inconspicuously lobed	lobed but not prominently	not lobed	not lobed	not lobed or inconspicuously lobed	not lobed	not lobed
Branchial tentacles	simple filiform	simple	compound	simple	simple filiform	simple filiform	simple	not known	simple club-shaped
Branchial sac.	not folded, stig. straight, internal longitudinal bars present	not folded, stig. curved, inter. long. vessels absent, papillae present	folded, stigmata irregular, internal long. vessels present	folded, stigmata absent, internal long. vessels present	not folded, stig. straight, no internal vessels	not folded, stig. spirally coiled, inter. long. vessels present	folded (rudimentary), stig. absent	not folded, stig. irregular, no internal vessels	not folded stig. absent, an irregular web of internal vessels
Dorsal lamina	languets	languets	languets	membrane	languets	languets	fold with fleshy lobes	membrane	languets? filiform
Viscera	simple loop right side	?	unknown	left side	behind branchial sac	on dorsal edge of branchial sac	an open loop, left side of sac	open loop on dorsal edge of branchial sac	close loop on dorsal (?) side of sac
Gonads	on loop of intestine	in intest-loop, left side	single mass right side ? close to endostyle	elongate mass one on each side, attached to mantle	in intestinal loop	single mass on intestinal loop	3 masses on each side attached to mantle	massive in loop of intestine ova 1.5 m. m.	massive, in loop of intes., ova 3 m. m.
Depth	1950 to 2600 fath.	7 fath.	2603 fath.	1600 fath. to 2603 fath.	shore	1375 to 2160 fath.	2633 fath.	600 to 2900 fath.	2182 fath.
Distribution	Australia	Terra del Fuego	Enderby Land	Enderby Land	many localities	South Pacific	Mid Atlantic	N. Pacific, Mid Atlantic	Coast of California

From this it appears that *Benthascidia michaelseni* is nearer akin to *Corynascidia* than to any other genus. But even so the differences in the branchial sac of the two are too great to permit them to be placed in the same genus. Even were we to imagine the retrogressive modification of the interstigmatic vessels of *Corynascidia* already so far advanced, continued to their complete obliteration, the internal vessels with their long triangular processes (see Herdman '82, pl. XXV, fig. 6) would still have no counterpart in the sac of *Benthascidia michaelseni*. I am not disposed to attach as much importance to the internal vessels and papillae of the sac as some writers have done, yet considering all the groups of Ascidians in which they occur, they certainly present a high degree of constancy, and to place together in the same genus two species one of which possesses true stigmata, internal vessels, and papillae, while the other has the vessels alone, would be to grossly violate the most reasonable view we have been able thus far to attain relative to Ascidian morphology and classification. But it is probable that more knowledge will find other good generic differences between *Corynascidia* and *Benthascidia*. The minute processes on the inner surface of the pharyngeal area of the latter are likely to be such. And in this connection attention may be again called to the irregular club form of the branchial tentacles. I have thought that the enlargements and irregularities might possibly be either the beginnings or the remnants of branches of compound tentacles. The conjecture rests however on meagre evidence. *Benthascidia michaelseni* I place then, pending more light on its structure, near *Corynascidia*, and without taking a definite stand on the merits of the somewhat divergent views recently expressed by Michaelsen and Sluiter relative to just how this and the several related genera should be grouped into families, should hold it to belong to the order Ascidiidae as recognized by Herdman. However, before dropping the question of the relationship of our species, I deem it worth while to call attention to the particulars in which it inclines toward *Clavelina*, or perhaps better the Clavelinidae. The large open, lobeless branchial orifice may first be noted; but should my interpretation of the branchial web as being without true stigmata (which I do not believe will happen) prove to be at fault, then we should

have to look to *Clavelina* for the sac most resembling that of our species.

Station 4390, Lat. 33° 02′ N., Long. 120° 42′ W., at the foot of the continental shelf, off San Diego; depth 2,182 fathoms, bottom gray mud.

It gives me pleasure to dedicate this new and in several respects specially interesting addition to the ascidian deep-sea fauna to Dr. W. Michaelsen, in recognition of his efficient studies on both littoral and abyssal tunicate life.

Ascidia clementea, n. sp.

Pl. 3, figs. 31 to 34.

General Characters.—Somewhat pear-shaped, the small end bearing the branchial orifice, turned to the dorsal side. Outline rather regular, and surface even. Area of attachment at posterior end, and to some extent on left side. Siphons distinct even in contracted state; probably prominent in life. Branchial turned to the dorsal side; atrial on the dorsal side about midway the length of the body. The lobes of both orifices large, the ventral ones (uppermost from the bent-over position of the siphon) of the branchial orifice, larger. Eight lobes to the branchial orifice, and six to the atrial (pl. 3, fig. 31). *Test* semi-transparent, thickness moderate and nearly uniform in all parts of the body, rather soft. Length of largest specimen 11 cm., greatest thickness 6 cm., distance between orifices 5.5 cm. *Musculature of mantle* nowhere highly developed, wholly wanting on most of the left side; the constituent fibers without regular arrangement.

Branchial Apparatus.—Branchial *tentacles* 75 or more, simple, filiform, and situated on the edge of a *broad, rather thick membrane or velum* (pl. 3, fig. 33) *t.c. Hypophysis* mouth horse-shoe shaped, the open end directed forward. The right horn turned in slightly in the specimen examined. *Gland* rather large, situated behind the hypophysis mouth a little more than its own length. *Ganglion* long and narrow, the anterior end immediately over the gland. The *peribranchial groove* narrow, outside the tentacular corona a distance about equal to the width of the membrane that carries the tentacles. *Dorsal lamina* a broad

membrane with numerous ribs on its sides, and short processes on its edge. Anteriorly the edge of the lamina is grooved for a distance about equal to the length of the combined ganglion and hypophysis gland (pl. 3, fig. 33). At its posterior end the lamina passes to the right of the mouth of the esophagus, and extends a full centimeter behind this point, and from its extremity a shallow groove turns back on the lamina and extends forward to the esophagus mouth.

Internal longitudinal vessels of branchial sac all of one size, and uniformly distant from one another, armed with strong *papillae* at the crossings of the transverse vessels, and also with smaller intermediate papillae. Spaces between the internal longitudinal vessels about equal to the distance between the transverse vessels, so that the meshes are nearly square. A rather pronounced horizontal membrane on the transverse vessels. Besides the ordinary transverse vessels, a system of very *large vessels*, or pipes (pl. 3, fig. 34), *t.b.p.*, on the external surfaces of the branchial membrane. These mostly running around the sac, but with occasional anastomosing longitudinal pieces. Typically about a dozen series of stigmata between two of these transverse pipes, but sometimes fewer. The diameter of a pipe equal to the space between two transverse vessels.

The branchial membrane with deep, narrow *plications*, these however not regular, and not involving the entire area of the membrane. Where the plicae are not present, about seven stigmata between two internal longitudinal vessels.

Digestive Apparatus.—Situated on the left side. The intestinal loop wide and simple, there being a slight curve only in the rectal part of the intestine. Stomach but little larger in diameter than the intestine, which is of very uniform calibre throughout its length. Wall of stomach with numerous, regular well defined folds. Esophagus very small. Renal organ voluminous, situated in the mantle, and covering over the entire digestive tract, extending considerably beyond it all around. Composed of a conglomerate of large clear vesicles, in the center of each of which is a yellow green body (pl. 3, fig. 32, *r.*)

Reproductive Organs.—Situated in the intestinal loop chiefly, but the ovary extending behind it somewhat. The ovary a retic-

ulation. Testis branched, situated on and immediately behind the stomach. Both oviduct and vas deferens following the course of the intestine to open into the atrial chamber near the atrial orifice (fig. 32, *ov.* and *t.*)

Several rather important variations from the type here diagnosed have been observed.

In some individuals the ribbing of the dorsal lamina, and the corresponding toothing of its edge, pertain to only the posterior half, or even less, of the membrane.

The great transverse pipes, or vessels of the branchial sac, are far less conspicuous in some specimens than in the one here figured. Again the plications of the branchial membrane are but feebly developed in some specimens. Finally, the renal vesicles are much less in volume in some than in others.

As the specimens in which I have observed these less pronounced expression of characters, as set forth in the diagnosis, were both considerably smaller than that from which the figures and diagnosis were made, it is possible that the differences are age or growth differences. This however, judging from our knowledge of life stages in some other ascidians, is hardly probable. It is more likely that we have to do with true individual variations.

It is probable that a genus will ultimately have to be formed to receive the species represented by the animal here described, but until more material can be examined it has seemed the wiser course to place it provisionally in the central genus of the ascidia group. The presence of a voluminous renal organ in the mantle is, of course, a violent shock to the best established characterization of the genus *Ascidia*. This, however, is the only character that favors an alliance with *Ascidiella*, the other recognized genus that calls for consideration in connection with it. In the distance of the ganglion and gland from the hypophysis mouth; the presence of a post esophageal extension of the dorsal lamina; and of intermediate papillae on the internal longitudinal vessels, the *Ascidia* as opposed to the *Ascidiella* affinities are clear enough, particularly if the count is to be on a numerical basis alone. As a matter of fact I am of the opinion that considerably more weight should be given to the position of the renal organ than to

any single one of the other characters above mentioned. It can hardly be regarded as weighty enough, though, to offset all the others.

The two particulars which, in connection with those that tend to break down the distinction between *Ascidia* and *Ascidiella*, will probably entitle the form to independent generic rank, are the broad muscular velum, or valve, that carries the tentacles; and the great external transverse vessels, or pipes, of the branchial sac.

Even in the genera like *Cynthia* and *Microcosmus*, where the "Tentakelträger" reaches its greatest development, I know of no other instance of its having a width and strength at all comparable with what we have here. Not only is it distinctly broader than the tentacles are long, but it is well provided with muscle fibers.

Although the large transverse vessels are not so unique as the tentacle carrier, corresponding as they undoubtedly do to the "vessels of the first order" in numerous other Ascidians, there appears to be no instance in which they are so large relatively to the other transverse vessels, and particularly where their position is so largely on the external surface of the branchial membrane.

In the wide, simple intestinal loop this species resembles *A. archaia*, Sluiter, but this is about the only character common to the two. Relative to the *Ascidiella* character of the renal organ, it may be recalled that Kiaer ('93 and '96) has pointed out that the disposition of these organs cannot be relied upon altogether for separating the two genera, since in *Ascidiella obliqua* of the Norwegian seas, they are restricted to the intestinal wall. Kaier consequently excludes this point from his definition of *Ascidiella*. One specimen was taken at station 4405, near San Clemente Island, 654-704 fathoms, April 9, 1905; and seven from station 4425 (see data under *Ciona mollis*).

Ciona mollis, n. sp.

Pl. 3, figs. 35 to 38.

External Characters.—Very soft and flabby, preserved specimens all in a collapsed and more or less shriveled condition. Form variable, usually somewhat longer than broad, but never

greatly so. Semi-transparent, the strong muscle bands of the mantle, and the digestive tract distinctly visible through the test. Siphons distinct though not long. Some of the specimens clinging to fragments of hexactinelid sponge by the posterior end and left side; others adhering to a compound ascidian, and still others to an anemone. Largest specimens about 2.5 to 3 cm. in length. *Test*, soft, transparent, rather thin, containing great numbers of cells, many of which are of peculiar granular character. *Mantle muscle bands* strong, usually six on each side, scarcely stronger on one side than the other, those running lengthwise of the body converging to a point at the posterior end of the animal (pl. 3, fig. 35); circular fibers in the siphons only.

Branchial Apparatus.—Siphons both at anterior end and not far apart, rather prominent, the atrial a little longer. Branchial with eight lobes (normally) and the atrial with six (normally).

Branchial tentacles numerous, more than 200, filiform, of several lengths, the longer and shorter not regularly alternating (fig. 36). *Hypophyseal mouth* simple, narrow-elliptical, the long axis extending radially with reference to the tentacular circle; *gland* on ventral side of ganglion, smaller than the ganglion. *Dorsal languets* finger-like with broad transversely expanded bases, rather close together. *Branchial sac* with both longitudinal and transverse internal vessels; also with stout papillae. Transverse vessels of two sizes, the larger crossing the stigmata at their middle, the smaller in pairs one each side of each larger vessel, both crossing the stigmata. Longitudinal vessels slightly larger than the smaller transverse ones. *Branchial membrane* proper, without folds, stigmata straight, long and narrow, in regular series, the vessels separating the series of two sizes, the larger and smaller alternating regularly. From four to six stigmata between each two internal longitudinal vessels (pl. 3, fig. 38).

Digestive Apparatus.—Situated on left side far toward the dorsum, general form that of an elongated open S. *Esophagus* short, *stomach* regular, elliptical in longitudinal section, the long axis usually about twice the length that of the transverse; wall regularly and closely plicated, the plicae about twenty in number; situated at the extreme posterior end of the body, the long

axis directed transversely to the antero-posterior axis of the animal. *Intestine* quite as long as the animal and of nearly uniform diameter throughout its length; anal opening near the atrial siphon, surrounded by about eight rounded lobes (pl. 3, fig. 35). No "*liver*" present.

Reproductive Organs.—Ovary a compact mass situated in the posterior loop of the intestinal S, near the stomach. *Testis* not seen. *Genital duct* (oviduct?) running parallel with the intestine to open near the anus.

The muscle bands of the mantle are of an unusual and striking character in this species. Their course and arrangement are indicated in the diagnosis and in pl. 3, fig. 35. The figure would give the impression that they are confined to the right side of the body, as they are, practically, in many of the Ascidiidae. This is not the case. They are as strongly developed on one side as on the other, and the number is in general the same on the two sides. Although they converge toward the posterior end of the animal in so pronounced a way, they do not fuse together at the point of confluence, a small area being left there about which the bands terminate abruptly. A feature about the bands not well brought out by the figure is the fact that the constituent fibers are disposed chiefly in two bundles or columns, so that each muscle has the appearance of being double. The breaking up of each muscle into several branches as it enters the siphon may be noted, but this is not unusual.

The branchial tentacles (pl. 3, fig. 37) contain within the lumen a series of narrowly pyramidal structures the bases of which are directed toward the thickened, grooved, narrower side of the triangular tentacle. These appear to be of a connective tissue, or secretive nature, but what their office may be it is difficult to understand. I do not know definitely of anything quite like these bodies in any other ascidian. Herdman '99 has shown (pl. Cyn. XV, fig. 5) a condition of the tentacles of *Styela persona* that may be similar, but in the absence of a statement in his text relative to the point, it is not possible to know how close the similarity is. It will be seen from fig. 36 that the tentacles are situated on a slight ridge. So far as I am able to determine there are from 225 to 250 of these tentacles.

There is considerable variation from the typical structure of the branchial sac as this is given in the diagnosis, and in the figure (pl. 3, fig. 38). The secondary or smaller transverse vessels are frequently absent. The primary transverse vessels while undoubtedly to be regarded as "internal" since they usually cross the stigmata, are as a rule less raised above the surface of the membrane than the figure gives the impression that they are. Furthermore there are considerable stretches on some of the stigmatic series where the primary vessels are absent.

The distally lobulated, enlarged, curved papillae deserve special notice. It will be seen that in general a single smaller projection occurs on the side of the papilla underneath the larger terminal lobe, or bent-over end of the papilla. In many cases there are two or even three of these lateral processes. The internal longitudinal vessels are distinctly more "internal" than are any of the transverse ones. It is interesting to notice that the longitudinal vessels are connected with the papillae some distance from their bases, and quite independently of any of the secondary lobes of the papillae. The interest in this fact lies in its possible bearing on the question of the secondary lobes attached to the papillae of some other ascidians, notably *Perophora*. It has been suggested that the secondary lobes in that genus are the remnants of internal longitudinal vessels. In the species now under examination we have the longitudinal vessels in full development, and secondary lobes on the papillae besides. I do not mean to imply by this that I should regard the secondary papillae in *Perophora* and in the present species as homologous. The condition now described does, however, show the possibility of secondary lobes on the papillae quite independently of the internal vessels.

The *dorsal languets*, about fifteen in number, are as shown in fig. 36 much broadened transversely and flattened antero-posteriorly at their bases. They are considerably farther apart toward the posterior end of the row than at the anterior. They are not situated on a membrane or other prominence.

From the posterior extremity of the long meandering endostyle, a shallow but distinct gutter continues on, nearly or quite to the esophageal opening.

In view of the fact that generally the viscera in *Ciona* extends unequivocally behind the branchial sac, it is important to determine precisely the relation of these parts in the present species, where apparently the viscera are alongside the sac. So far as concerns the specimen represented in fig. 35, it would appear that it actually falls short somewhat of reaching back to the posterior limit of the body. In a majority of the specimens of the collection the digestive tract was in quite a different relation to the sac from that here shown. It was thrust out dorsally and somewhat posteriorly as compared with its position in the specimen figured. This condition I have supposed to be unnatural, probably due to pressure of some sort. As a consequence the specimen figured was selected because it was believed to be more nearly normal as regards artificial distortion than any of the others. I am inclined to believe that some of these others, could they have been examined before contraction and distortion, would have been found to conform somewhat more closely to the usual Ciona type of viscera than did the one figured.

Although the present species is very distinct from any *Ciona* hitherto described, there can hardly be a question as to its generic affinities. It is true that the viscera extend but slightly if at all behind the branchial sac and that this character has usually been regarded as a rather important one for the genus. In view, however, of the fact that in all other respects, unless possibly in the number and structure of the branchial tentacles, its Ciona traits are so positive; and in view of the further fact that probably in life the viscera do here extend somewhat behind the sac, and that in at least one other species of the genus, viz., *C. savignyi* Herdman, the backward extension of the viscera is not great, I have felt no hesitation in assigning *moll's* to this genus.

About a dozen specimens were taken all at one haul at Station 4425, 21.8 miles S. 7°E. of the east point of San Nicolas Island, 1100 fathoms, on bottom of green mud, sand and globigerina.

Cystodites cretaceous? v. Dr.

A large quantity of a fine representative of this genus, closely related to *C. cretaceous* v. Dr., comes from the vicinity of Monterey Bay. Although there are a dozen colonies, or perhaps pieces

of the same colony, the largest of which is not less than 15 cm. across, I am still unable to decide positively what to do with the species systematically. From what evidence I can get I can not differentiate it from Drasche's Mediterranean species. In color, size and general characters of the colony it appears to agree almost perfectly with that species. I think, too, the spicules are practically alike in the two. However, there is some doubt on this point, since very few of what I suppose to be the natural spicules are present in the specimens. The cellular portions of the spicule cases, and also calcareous matter, are abundant enough, but the calcium carbonate is in the form of minute, long, slender crystals, instead of being the usual Cystodites discs, though a very few of the latter have been found. My conclusion is that the original spicules have been destroyed, probably by the formaldehyde in which the specimens are preserved, and some of the calcium carbonate recrystallized in the form in which it now appears—though why this recrystallization should have taken place is not obvious.

As to the zooids, they are everywhere so excessively contracted that, in spite of much effort, I am unable to get at anything more than their general features. So far as these go, I can not distinguish the specimens from *C. Delle Chiajae* v. Dr., Neapolitan specimens of which I have compared them with; and from Lahille ('90) I learn that, so far as the zooids are concerned, *C. Delle Chiajae* does not differ in any essential way from *C. cretaceus*. On the whole, the zooids of my colonies are somewhat larger than are those of *C. Delle Chiajae,* but the difference may easily be due to the fact that the specimens from Naples are preserved in alcohol, while the Californians are in formaldehyde. The milk-white of the zooid capsules and the transparency of the remaining parts of the test are the facts that make me associate these specimens with *C. cretaceous* rather than with *C. Delle Chiajae.*

I think it is rather probable that when specimens of the California species are obtained in such condition that all their characters can be made out, a new species will have to be formed for them. Under present conditions, however, I must leave the point in doubt.

Station 4463, Point Pinos Light S. 17°W. 8 miles, May 13, 1904, 111 to 41 fathoms, rocky bottom.

Psammaplidium spauldingi, n. sp.

Pl. 3, fig. 39.

General Characters of the Colony.—Expanded, loosely adherent by whole under surface, top smooth but undulating, hard from great quantity of sand, which is uniformly disseminated through the whole test. Edge of the colony rolled up a little. The small zooids numerous, evenly distributed, no systems (?), each branchial orifice marked on surface of colony by a small papilla. Color uniform grey, due to the imbedded sand.

The single colony taken, 6 cm. by 5 cm. in its greatest dimensions and 1.8 cm. thick in thickest part, though considerably thinner in most places.

Zooids.—Abundant, long, slender and nearly straight, the thorax but little thicker than the abdomen and long post-abdomen. Thorax about 3 mm. long; abdomen, before contraction, probably about 2 mm.; post-abdomen variable, but several times as long as thorax and abdomen combined. Mantle containing a few slender longitudinal muscle bands which extend far down into the post-abdomen.

Thorax.—Branchial orifice on prominent siphon, six-lobed, atrial situated well back—a distance from the end of the branchial siphon about equal to the thickness of the thorax. Atrial orifice beset with a moderately long languet, this usually undivided, but occasionally bifid at tip. The long cylindrical sac with about eighteen series of short stigmata, muscle bands in interstigmatic series well developed. Endostyle large and tortuous. Branchial tentacles about ten, unequal in length, some of them quite long.

Digestive Apparatus.—Loop narrow, esophagus about equaling the stomach in length, and also about equal both in thickness and length to the pyloric portion of the intestine. Stomach with three or four large longitudinal folds or lobes. A distinctly set-off enlarged section of the intestine following the pyloric portion. Ascending rectal limb of the intestine straight, uniform in diameter and parallel with the descending limb.

Gonads.—Far behind the intestinal loop in the post-abdomen,

the testes further back and disposed in a number of spherical lobes.

This species falls into the section of the genus in which the zooids are long, slender and uniform in outline, and with *P. obesum* (Sluiter 1898), from the South African coast, represents about the extreme in this direction. In the character of the atrial languet and stomach folds, however, these two species are distinctly differentiated from each other.

A single colony, Station 4420. (See data under *Didemnum opacum.*

Didemnum opacum, n. sp.

Pl. 3, figs. 40 and 41.

General Characters of the Colony.—Narrow elongate (in the single specimen seen), thickness varying in different parts from 1 mm. to 3 or 4 or 5 mm. in places where well defined, rather pointed pyramidal elevations are present. Prevailing color dull brown with traces of green, but where the brown is absent the test is made white by the closely crowded calcareous spicules. Position of the zooids for the most part distinct by reason of the absence of the spicules which are very abundant in all the surrounding test. *Zooids* rather crowded, evenly distributed, no common cloacal orifices on the colony at hand. Length 3.5 cm., width in broadest part 1.3 cm. Attached by whole under surface to a fragment of silicious sponge. *Spicules* very abundant, especially concentrated in a thin layer slightly beneath the surface of the test, but scattered through the whole test, of the stellate form characteristic of the genus, but irregular in both size and conformation, the rays varying from pointed to truncate, and presenting always a more or less positive striate appearance. A massing of spicules into three distinct groups about the branchial orifice of the zooids, clearly visible to surface inspection of the colony as three white bodies equally spaced around the orifice.

Zooids.—Small, much contracted, probably not more than 2 mm. long when fully extended, thorax and abdomen seemingly of about equal length and not very sharply set off from each other; *Mantle muscle-bands* few, running obliquely backward from the anterior end.

Branchial Apparatus.—Siphons both distinct, the branchial longer, its six lobes varying from long and pointed to low and broad. Atrial very far back, obscurely six-lobed. Three rows of stigmata, each row on each side containing about twelve long, narrow openings. No considerable area of unperforated branchial membrane at either end of the sac. *Endostyle* heavy, tortuous, even in the least contracted specimens.

Digestive Apparatus.—Intestinal loop rather narrow, hardly broader than the thorax; stomach elongate globular, smooth-walled; a distinct pyloric section of the intestine, whole intestinal wall containing much brown pigment. Abdomen frequently but by no means always severed from the thorax in the preserved colony.

Reproductive Organs.—Only the ovary seen, this consisting of apparently a few large ova situated alongside the posterior end of the intestinal loop. *Tadpoles* very large, considerably exceeding in bulk the adult zooids. The adhesive tubes, and so-called "gemmiparous tubes" especially well developed; of the former three, the seemingly usual number, being present; of the latter there are typically six, all large, trumpet-shaped and closely crowded.

The zooids are so much contracted and so opaque in the single colony of this species that, in spite of much effort, I have been unable to make the examination as complete as desirable. Enough has been determined, however, to forbid its being identified with any species hitherto described. Its distinctness depends rather on the combination of several characters than on the positiveness of any. For example, the extremely far back position of the atrial siphon would not in itself be a character of sufficient importance to debar the species from several other members of the genus. When, however, this trait is taken together with the length of the siphon, its rather obvious lobing, it seems to become a good character. The absence of unperforated areas of branchial membrane at either end of the sac is also distinctive when joined with other trivial characters. The number of "gemmiparous tubes" of the tadpole is greater than in the young of any other species of which I have found figures of the larvae.

On the whole I should regard this species as more closely related to *D. sargassicola* Giard than any other, but Lahille ('90), from later studies of this species, considers it as not specifically distinct from *D. cereum* Giard, and from this latter our animal differs in several important respects.

Station 4420, east point of San Nicolas Island S. 77°W., 3.8 miles, April 12, 1904, 33 fathoms, bottom fine gray sand.

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ABBREVIATIONS.

a. l.—Atrial languet.
b. c.—Body portion of column.
b. f.—Branchial folds.
br. o.—Branchial orifice.
b. m. v.—Vessels from branchial sac to mantle.
br. s.—Branchial sac.
b. t.—Branchial tentacles.
d. l.—Dorsal lamina.
d. ln.—Dorsal languets.
end.—Endostyle.
g.—Gland.
g. i. f.—Groove of intratentacular field.
gl.—Ganglion.
h. f.—Holdfasts.
hv. m.—Hypophysis mouth.
i. l. v.—Internal logitudinal vessels.
inf.—Infundibulum of branchial sac.
i. p.—Papilla of branchial membrane.
m.—Mantle.
ov.—Ovary.
p. b.—Papillary band of test.
p. g.—Peripharyngeal groove.
p. i. f.—Papillae of intratentacular field.
p. v.—Primary vessels of branchial sac.
r.—Renal organ.
s. d.—Sperm duct.
s.—Stomach.
t.—Testis.
t. b. p.—Transverse branchial pipes.
t. c.—Tentacle carrier.
t. ?—Tentacles of doubtful significance.
tst.—Test.
t. v.—Internal transverse vessels of the first order.
t. v.[1]—Internal transverse vessels of the second order.

EXPLANATION OF PLATES.

PLATE I.

Figs. 1 to 6.—*Halomolgula ovoidia.*

Fig. 1. Whole animal, natural size—a rather large specimen.

Fig. 2. Surface view of the test surrounding the branchial orifice, showing the arrangement of the papillae.

Fig. 3. A few of the papillae, considerably enlarged.

Fig. 4. A tentacle of the first order.

Fig. 5. The ganglion, hypophysis, and meandering course of the pharyngeal band, dorsal view.

Fig. 6. One side of a branchial fold. Some of the stigmata are more elongate and curved than any shown in this figure.

Figs. 7 and 8.—*Molgula regularis.*

Fig. 7. Lateral view of the animal removed from the test. ×2.

Fig. 8. Ganglion and surrounding parts seen from inside the branchial sac.

Figs. 9 to 16.—*Halocynthia okai.*

Fig. 9. Whole animal, natural size.

Fig. 10. Branchial orifice, × 2.

Fig. 11. One of the large spines, × 3.

Fig. 12. A smaller spine without terminal whorl of spinelets, × 3.

Fig. 13. Two of the short whorled spines, × 42.

Fig. 14. A single tentacle.

Fig. 15. Small portion of the branchial membrane, inner surface.

Fig. 16. Scheme of a section of a branchial fold.

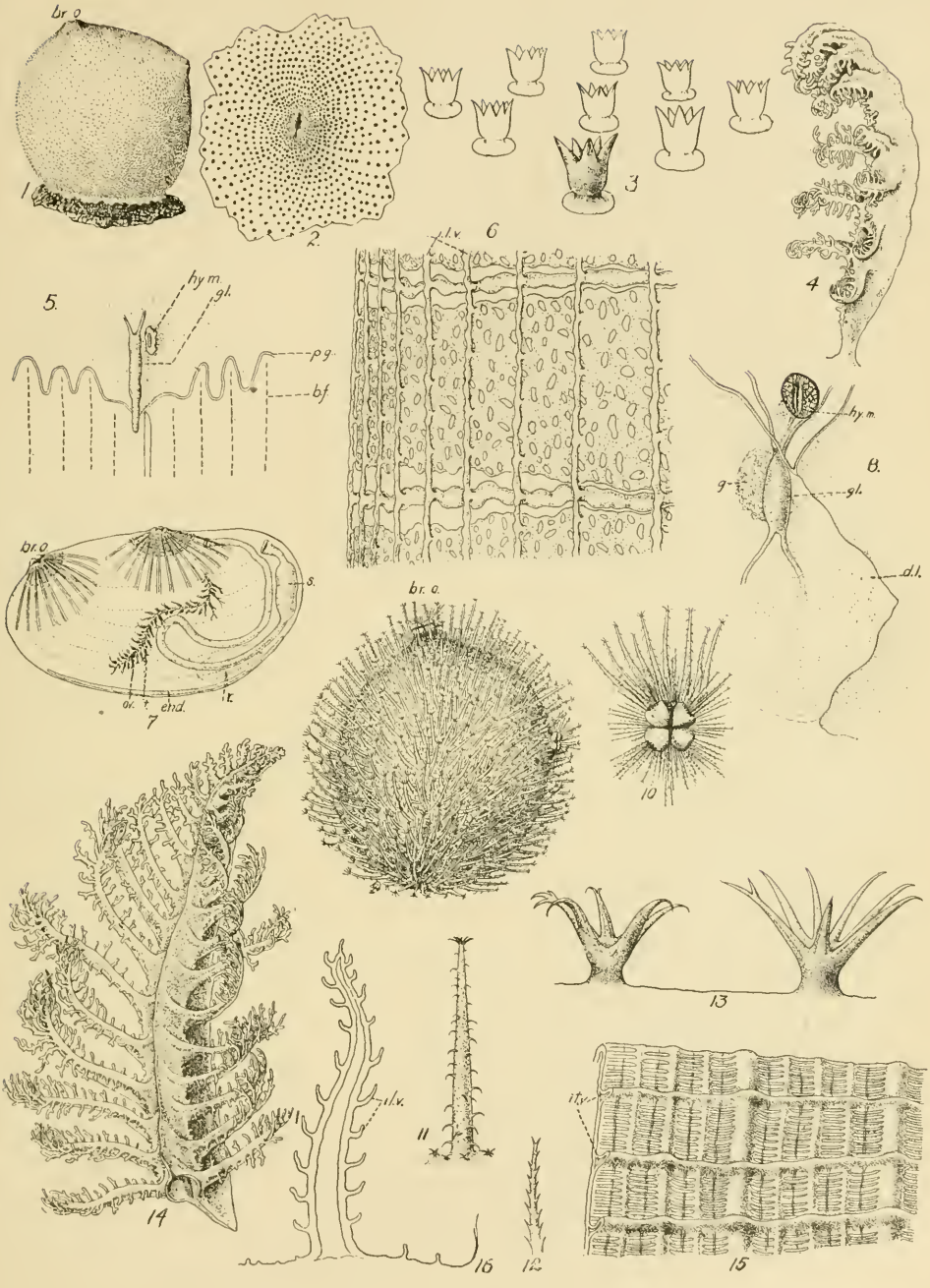
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PLATE 2.

Figs. 17 to 19.—*Boltenia echinata.*

Fig. 17. The whole animal from which the description is mostly drawn, × 1.

Fig. 18. One side of a branchial fold of the specimen shown in figure 17.

Fig. 19. The whole animal, a specimen from near Point Loma, that shown in 17 being from near Point Pinos. × 4.

Figs. 20 and 21.—*Culeolus pyramidalis.*

Fig. 20. Side view of the whole animal, × 1.

Fig. 21. Dorsal view same specimen, × 2.

Figs. 22 and 23.—*Microcosmus transversus.*

Fig. 22. Side view of the whole animal, × 1.

Fig. 23. The same specimen removed from the test and the mantle cut open and laid back, × 1.

Figs. 24 to 29.—*Benthascidia michaelseni.*

Fig. 24. The column with holdfasts, × 2.

Fig. 25. A small tuft of the holdfasts, × 12.

Fig. 26. Some of the mantle musculature in the region of the supposed branchial orifice.

Fig. 27. The digestive apparatus and sexual organs, × 1.

Fig. 28. Outline of the digestive tract, showing the tuft of filiform appendages near the esophageal orifice and a fragment of the branchial membrane attached.

Fig. 29. A portion of the tentacular circlet and hypophyseal region seen from within.

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PLATE 3.

Figs. 30 to 34.—*Ascidia elementca.*

Fig. 30. A fragment of the branchial network.

Fig. 31. The whole animal, × 2.

Fig. 32. The animal removed from the test, showing intestinal tract, reproductive organs and "kidney."

Fig. 33. Hypophyseal complex, dorsal lamina, and tentacular cirelet seen from within.

Fig. 34. Small piece of branchial membrane with two of the large transverse vessels.

Figs. 35 to 38.—*Ciona mollis.*

Fig. 35.—The animal removed from the test, × 2.

Fig. 36. Hypophyseal region with dorsal languets and a portion of the tentacular circlet.

Fig. 37. A single tentacle.

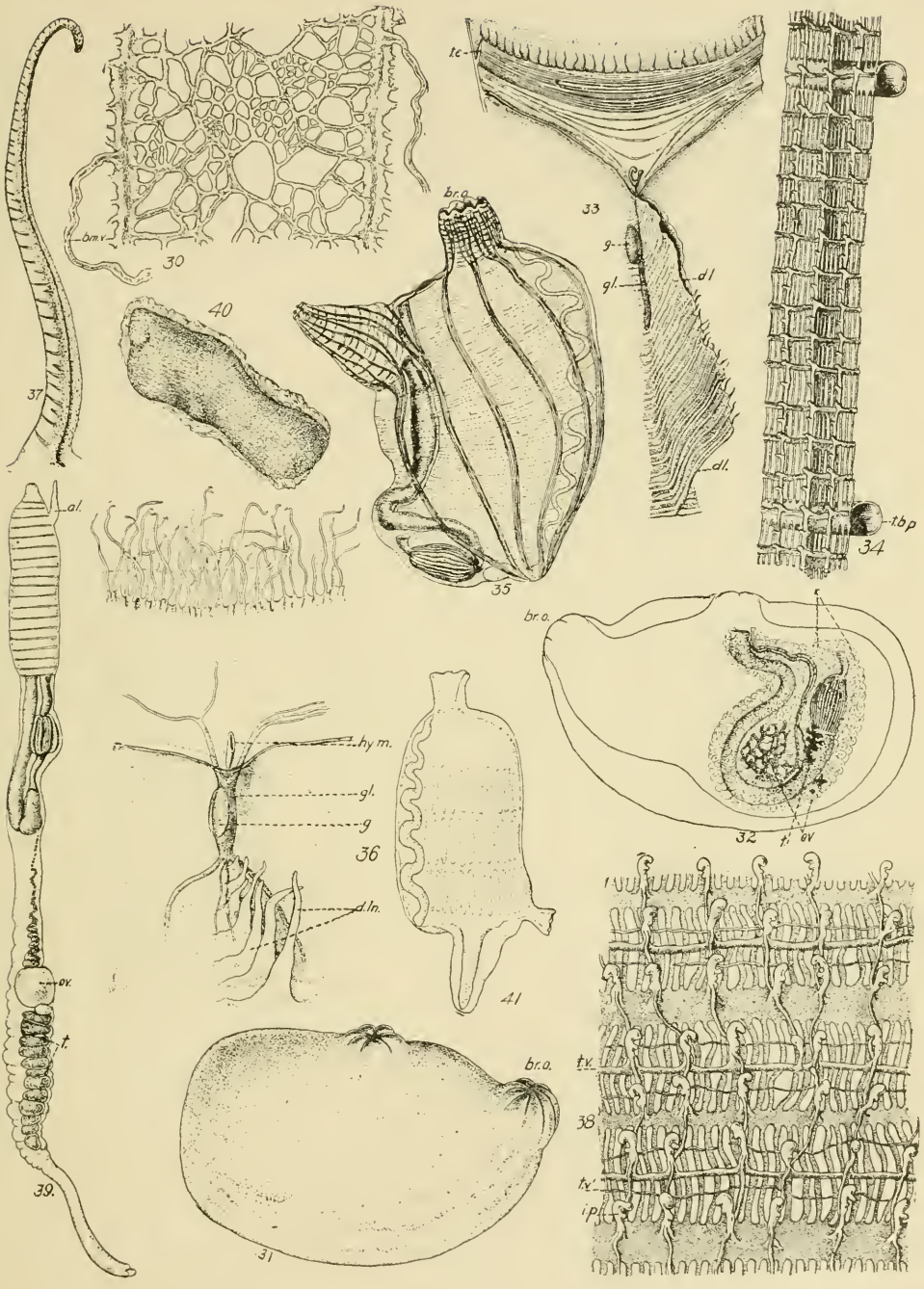
Fig. 38. Portion of the branchial membrane, inner surface.

Fig. 39. A zooid of *Psammaplidium* Spauldingi, × 20.

Figs. 40 and 41.—*Didemnum opacum.*

Fig. 40. The colony × 1.

Fig. 41. A branchial sac much enlarged.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OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

BEHAVIOR OF THE STARFISH *ASTERIAS FORRERI* DE LORIOL

BY

H. S. JENNINGS

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BEHAVIOR OF THE STARFISH, *ASTERIAS FORRERI* DE LORIOL

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CONTENTS.

PAGE

Introductory 56
The nature of the problems of behavior; behavior as regulation 56
Behavior of the starfish 58
Species studied. Plan of investigation.
Respiration and its protection by the pedicellariae 59
Method of respiration 59
The pedicellariae 60
Their action in protecting the gills 60
Capture of crabs, etc. 63
Detailed behavior of the pedicellariae 64
Kinds of pedicellariae 65
Action system of pedicellariae 66
The attack 67
Varied reactions 68
Effects of different stimuli 69
Opening, closing and grasping 70
Closing 74
Length of time that the jaws remain open 76
Time of holding 76
Pedicellariae of the rosettes 76
Large solitary pedicellariae 78

PAGE
Seizing parts of the starfish ... 78
Independent reactions and transmission of stimuli ... 79
Influences determining variation and modification of reactions in the pedicellariae ... 82
Capture of food ... 84
Introductory ... 84
Typical case of food capture ... 85
Animals used as food ... 87
Combat between starfish and sea urchin ... 88
Capture of large living fish ... 89
Nature of stimuli causing the food reaction ... 91
Food pulled away from pedicellariae by the tube feet ... 92
Feeling about in search of food ... 93
Conveying food to the mouth ... 93
Action of the stomach in taking food ... 94
Behavior of the starfish in selecting the conditions of existence ... 94
Introductory; necessity of selecting proper environmental conditions 94
Exploratory movements ... 95
Adaptiveness of the movements ... 96
Current erroneous explanation of the negative reaction ... 96
Method of locomotion in the starfish; erroneous current view ... 98
Three classes of protective reactions ... 101
Reaction to light ... 102
Movement away from the light ... 103
General stimulating effect of increased light ... 104
Movement toward darker regions, and coming to rest in the shade ... 104
Direction of rays versus differences in illumination ... 105
Position taken when confined in a uniformly illuminated field ... 108
Effect of light on the righting reaction ... 110
Vision in the starfish? ... 110
Positive reactions ... 113
Factors determining the nature and variations of the reactions to given external stimuli ... 114
Interaction and interference of stimuli ... 114
Effects of position of the body ... 115
Persistence of impulse to move in a certain direction ... 115
Effect of previous stimuli ... 117
Effects of physiological condition; reaction to situation as a whole 118
The righting reaction ... 120
Previous work ... 121
Variability (Preyer) ... 121
Driesch's formulation ... 122
Plan of present account ... 123
Designation of the rays ... 123
Variability ... 125
Different types of the reaction ... 125

PAGE
Irregular reactions 129
Diverse methods of beginning the reaction 132
The righting impulse 132
Determination of actions before the impulse 135
Factors in determining the direction of the impulse 135
Light 135
Structural differences in the rays 136
Rays that first come in contact with the substratum 136
Side of the ray that first comes in contact 137
Tilting of the body 137
Contact with an object 137
Rays that first become attached 138
Number of opposed attached rays 138
Relative number of tube feet attached in different rays 139
Coordinated position and action of the rays 139
Experimentally releasing certain rays 140
Intense stimulation of certain rays 141
Impulse retained from previous reaction 141
Impulse present before the animal is turned 141
Permanent tendency to turn toward a certain pair of rays 142
Summary on the righting impulse and the factors determining it 145
Persistence of the impulse 145
Changing an established impulse 146
Indecision 147
Formation of Habits in the starfish 148
Habits in other lower animals 149
Nervous system of the starfish 149
Definitions of habit 149
Preyer's work on "intelligence" in the starfish 150
Preyer's work on the brittle star 151
Why Preyer called the behavior "intelligent" 152
Glaser's negative results 153
Negative results of the present author 154
"Versatility" of the starfish as possible cause of lack of habit formation 155
Conditions required for habit formation 155
Method for training the starfish 156
Experiments in training the starfish 156
Positive results 168
Nature of the habits formed 168
Why habits are not readily formed 168
Why they soon disintegrate 169
The unified impulse and the determination of the varied activities under its influence 169
The problem 170
Effect of external conditions 171
Action of parts in the interest of the whole 171

PAGE
Restatement of the problem 173
Proposed solutions; Driesch's doctrine of the entelechy 174
A physiological formulation 175
The difficult point; two possible answers 177
Development of the unity of action 177
Imperfect unity 178
Imperfect present solution of the problem on purely physiological grounds 179
The entelechy doctrine a renunciation of all solution 179
The problem one whose solution is to be completed in the future 182
Concluding statement 183
Literature cited 184

INTRODUCTORY.

An organism is a complex mass of matter in which certain processes are taking place; the aggregate or system of these processes we call life. The fundamental processes are those that we call metabolism. Every animal is continually taking in certain kinds of matter, transforming them, and giving them off again to the outside—gaining energy in the process. Subsidiary to this general chemical transformation we find the processes of digestion, circulation, excretion and the like. It is of the utmost importance, if we are to understand the behavior of organisms, that we think of them as dynamic—as processes, rather than as structures. The animal is something happening.

In connection with these internal processes, we find that most organisms have a system of movements, of the body as a whole, or of its external parts. This system of movements we call *behavior*. It is closely bound up with the internal processes; indeed, the two sets of activities are really one, and we shall be led far astray if we try to think of the behavior separately from the internal processes. In two ways the behavior shows itself an outgrowth of the internal processes. First, the energy for the external movements is all produced in the internal processes, so that change in the processes necessarily involves change in the movements; and change in the movements demands a previous change in the internal processes. The two then can not obey

essentially different laws. Second, the movements of organisms form a system which is of such a nature as to assist the internal processes and keep them in progress even under unfavorable and changing conditions. Behavior is the method of regulating the internal processes by means of external movements. To keep the internal processes going, the animal must do certain outward things. Thus behavior and the internal processes are not two things; they are a unit and can not be understood separately. The regulatory character of behavior has been so clearly demonstrated by recent studies in both higher and lower animals[1] that no apology is required for frankly making it the basis for an account of the behavior of a given animal; this we shall do in the case of the starfish.

The unity of the internal processes and behavior is very evident if we include in behavior such movements as the expiration and inspiration of air, the movements of the stomach and intestines in digestion, the beating of the heart, and the like. But it is scarcely less evident in the movements which animals make in search of pure air, of food and of other things necessary to keep the internal processes going. These movements make up a large share of behavior in man as well as in other organisms.

Furthermore, in order that the internal processes constituting life shall be kept in progress, the organism must be retained in certain favorable conditions, and kept out of others that impede the processes. It must not be allowed to become too hot or too cool; it must not be poisoned nor crushed; it must not be devoured by enemies. Strangely enough, we find the movements of all organisms to be of such a character as tends to keep the creature under favorable conditions, to protect and defend it. Sometimes they fail, and the failures are as interesting as the successes.

The general problem of physiology is: How are the bodily processes kept going? The special problem of behavior is: How are the bodily processes kept going by the aid of movements? And how does it happen that the movements are of such a character as to keep the processes going?

[1] See Jennings, Behavior of Lower Organisms (New York, 1906).

Behavior of the Starfish.

We propose in the present paper to study the problem of behavior in the starfish. The behavior of starfishes has been much studied, particularly by Preyer (1886) and Romanes (1885), though many others have published observations on these animals. The work of Preyer is one of the best and most careful studies that has ever been made of the behavior of a lower animal. But many of the facts have been left unknown, many important questions unsettled. New problems have arisen, and the study of behavior has entered on a new phase since the time of Preyer and Romanes. Examination of recent works touching animal behavior reveals a number of specific problems in starfish behavior on which thorough study is much needed. Thus Driesch (1903) has made the righting reaction the basis of most interesting discussion leading to wide-reaching conclusions, and Driesch himself points out the need of a renewed thorough study of the matter. To this special attention is devoted in the present paper. Loeb (1900) has given marvelously simple explanations of such reactions of this animal as are seen in fleeing from an injurious stimulus,—explanations which would have astounded Preyer and Romanes; and has contradicted various observations and conclusions of Preyer (Loeb 1900, p. 65), so that these matters require re-examination. Various investigators have pointed out the interest of a study of the behavior of the starfish with relation to the possibility of the formation of habits. V. Uexküll made a thorough study of the behavior of the pedicellariae of the sea urchins; similar work is needed for the starfish.

In view of these facts, the writer took the opportunity afforded by a summer at the marine laboratory of the Marine Biological Association of San Diego, at La Jolla, in southern California, to make a renewed study of the behavior of the starfish. Thanks are due to the Marine Biological Association of San Diego, and especially to Professor C. A. Kofoid of the University of California, who was in charge of the laboratory in the summer of 1906, for lending every possible assistance in the work.

Many starfish are found near the Station; the commonest

species, *Asterias* (*Coscinasterias*) *forreri* de Loriol[2], was selected for special study. Nothing has been published heretofore on the habits and behavior of this species.

Asterias forreri is found on the under side of rocks, just below the tide level. It clings closely to the rock, and usually moves little or not at all while under the observation of the curious, so that at first there appears to be little behavior to study.

How does such a creature manage to succeed in the struggle for existence? How does it get material to keep up the processes of metabolism? How does it happen to remain under such conditions as enable the life processes to continue in the midst of thousands of agencies that are acting against these? By taking up the behavior from this standpoint we shall be able to weld what might be mere scattered observations, into a connected whole. At the same time this will perhaps give us some insight into the complex life of the sea-shore and the manifold interrelations of its inhabitants.

Respiration and its Protection by the Pedicellariae.

The first of the life processes which we shall take up is that of respiration. The starfish, like man and *Amoeba*, must have pure oxygen, or its life processes stop. If left in water that is not aerated, it dies in a few hours. How does the starfish get its oxygen?

The body of the starfish is protected by a basket-work skeleton of lime, which bears over its upper surface many short spines. Between the meshes of the basket-work there are holes, which are covered in the living starfish by a delicate membrane. If in the living animal we examine the surface between the spines, we find these little patches of membrane covered by many small finger-like processes (fig. 1 *g*.) These processes, of which each starfish bears many hundreds, are the gills of the animal. They are hollow and have very thin walls. Their internal cavity opens into the body cavity of the starfish, which is filled by a colorless fluid. This fluid circulates within the finger-like gills, passing up one side to the tip, and down the other. This circula-

[2] Kindly determined for me by Dr. Hubert Lyman Clark.

tion may be easily seen if one thrusts a pointed pipette containing some finely ground India ink through the body wall of the starfish and injects the ink into its body cavity. With a lens the particles of the ink are seen circulating in the gills[3]. The circulation is due to the lashing of fine cilia which line the interior of the gills.

On the outer surface of the gills the sea water likewise flows rapidly toward the tip of the gills, driven by cilia on the surface. Thus on the inside of the thin wall of the gill there is a continual supply of new body fluid; on the outside a continual fresh supply of sea water, laden with oxygen. Through the thin membrane the oxygen passes from the water into the body fluid, just as it passes through the thin membrane of our lungs into our blood.

This is evidently an effective method of obtaining fresh oxygen, yet it exposes the starfish to various dangers. All its other soft structures are protected by the hard spiny shell, but the delicate gills are on the outside of the body. It is as if we had our lungs outside instead of inside our bodies; evidently they would be dangerously exposed. And in the starfish, as in ourselves, the respiratory organs are most essential as well as most delicate structures. They must be protected if the other life processes are to go on.

Serving mainly for the protection of these gills, the starfish has developed a most extraordinary set of organs, known as the pedicellariae. These, as is well known, are small jaw-like structures. If we examine closely the outer surface of the starfish, we find surrounding the base of each spine a fleshy ring, often colored, in which are imbedded a large number of small whitish oblong bodies having a cleft down the middle (fig. 1, p). These are the pedicellariae. In the starfish at rest, these are shrunken down into the flesh of the ring, and show little indications of their real character.

Now let us disturb a group of the gills of the starfish in some

[3] Ink or other foreign substances thus injected are later gotten rid of by the gills in the following way. The ink particles, circulating in the gills, are caught near the gill tips, so that in time the tips are filled by a black mass. Now the tip of the gill becomes soft and gelatinous, and finally melts away, allowing the ink to float off in long strings into the water. The gill then closes at the tip. This remarkable process is easily observed; it has been noted by others (Durham, 1888; Cuénot, 1902).

way, either by touching them with a bristle, or by causing some small animal, such as a crustacean, to creep over them. The gills at once collapse and shrink down close against the surface of the starfish, where they are less likely to be injured. And now, after they have received one or two jabs by the bristle, or by the claws of our crustacean,—we suddenly see the ring which surrounds the base of the neighboring spines rise upward to the top, so that the spine is completely hidden. At the same time each of the small oval bodies extends outward a distance on a short stalk and opens widely by a cleft down its middle. We now see that each is a pair of broad jaws, with sharp teeth. Under

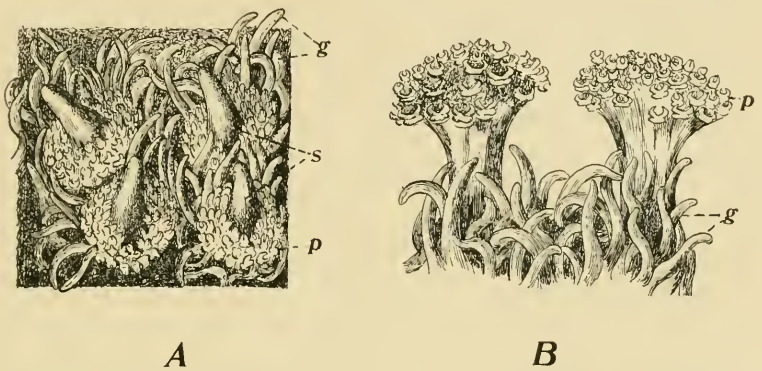


Fig. 1.—Portions of the surface of the starfish, showing the gills (g), the spines (s), and the pedicellariae (p). A shows the condition in the unstimulated animal, in which the rosettes are retracted and the pedicellariae closed. In B the rosettes of pedicellariae have risen to the top of the spines and the jaws are opened.

a lens the rising ring looks like some hundred-handed or hundred-jawed monster, each jaw gaping widely and ready to attack (fig. 1, B). A half dozen or more of these rings, belonging to the spines immediately surrounding the region where the gills were disturbed, thus rise.

At the same time the spines all bend over toward the spot where the disturbance is occurring, so as to form a close ring of hundreds of these widely-opened jaws; they almost completely cover the invaded region. A number of them are thus certain to strike against the creature causing the disturbance, so as to find some part of its body between the jaws. These at once snap

together like a vise and hold on tightly, the numerous teeth which each pedicellaria bears enabling them to hold on without slipping. And now the little animal thus seized begins to struggle and kick. This enables the other batteries of pedicellariae to locate him still better. The spines bend more precisely toward the point of disturbance. And even the individual pedicellariae of a given ring search out more or less independently the offending object. If something rubs against the base of a spine on one side, beneath the ring of pedicellariae, the jaws of that side of the ring bend down and reach out precisely toward the base of the spine, seizing whatever they find there.

Thus in a short time every appendage, every hair, every movable part, of the intruding crustacean has been seized by from one to a score of these jaws. They hold on stoutly, so that the little animal is held absolutely quiet; though still living, it can not move any more than a wooden animal. Sand fleas, small shore crabs, or any other small animals having appendages that can be seized are thus reduced in a minute or two to absolute immobility.

And now the delicate gills come out of their hiding, extend themselves in despite of the little animal that had clawed them so violently, and continue unhindered their work of aerating the body fluids. The small animal disturbs them no more, for he is held thus immobile by a hundred vises till he actually dies and falls to pieces, so that there is nothing more to hold to. There is absolutely no hope for such a creature as the sand flea (one of *Gammaridae*), when it has thus been seized by the pedicellariae. To attempt to crawl over the surface of the starfish is certain death.

The pedicellariae thus serve as a most effective protection for the gills; they completely prevent any serious disturbance of their functions on the part of small predatory organisms. I have seen great numbers of small crustaceans thus caught and held by the pedicellariae. If one watches for a time a starfish that has been placed in an aquarium containing many small crustacea, he quickly realizes how important is the function of the pedicellariae in thus preventing all injury to the delicate respiratory organs. This is in the species of starfish we are considering,

undoubtedly their chief function. Cuénot (1887) describes briefly a similar action of the pedicellariae in *Asterias glacialis;* he observed that small worms were seized and held immobile by them till they died.

The protective activities of the pedicellariae are not by any means limited to very small organisms. While even copepods less than a millimeter in length are seized and held, larger sand fleas and other crustaceans, a centimeter or more in length, furnish the commonest examples of their effective activity. And even much larger crabs are dealt with in an equally effective way. Shore crabs are very numerous on the rocks where the starfish are found, exploring actively in search of garbage or suitable prey. These vary in size from less than a centimeter in width, up to ten or fifteen centimeters. These crabs frequently attempt to run over the surface of the starfish, or to pluck off its gills as tender morsels of food. Any of these crabs, up to perhaps three centimeters in diameter, is held by the pedicellariae in the way we have described. The crab often fights savagely with his large claws, and manages to do considerable damage, pulling off a few score of the pedicellariae before he is rendered immobile. But his limbs are so studded with hairs that his liliputian adversaries are able to seize him in a thousand places, and in a short time he is compelled to succumb. I have often seen crabs two or three centimeters across thus held quiet for days at a time by a starfish upon which they had unluckily ventured.

Into the large basin where the starfish were kept, a considerable number of the sand crabs, *Hippa analoga* St., were placed. These are two to three centimeters in length. They were quickly captured by the starfish. Fig. 2 is a photograph of a starfish that had thus captured four of these *Hippas* and one of the shore crabs. The five crabs remain immovable, attached to its dorsal surface.

As may be judged from these facts, the pedicellariae hold with much strength. This may be easily shown as follows: The back of the hand is pressed against the dorsal surface of a starfish. The pedicellariae seize the hairs of the back of the hand and the starfish may now be lifted completely out of the water by means of them. They are thus able to support the animal's own weight in the air.

If still larger crabs or other animals come against the starfish they quickly withdraw after being seized by a few score of the pedicellariae. Often, of course, the animal carries away a number of the jaws.

It is clear therefore that in this species of starfish the pedicellariae are important defensive organs, playing the chief part

Fig. 2.—Starfish holding six crabs which have been caught by the pedicellariae. (The five white Hippas are easily seen; the other crab is dark in color, and is on the disk of the starfish.) Photograph.

in protecting the starfish from predatory enemies. They are specially serviceable in protecting the delicate gills; through their prompt and effective action it is almost impossible for the gills to be disturbed in their important functions.

Detailed Behavior of the Pedicellariae.

It will be worth while to study more carefully the behavior of these remarkable protective organs. The pedicellariae make almost the impression of independent animals; indeed, it was at one time held that they were parasites on the starfish. They have a system of behavior as complete as that of many of the lower

animals, though it is directed mainly toward conserving the welfare of the starfish as a whole, rather than toward the preservation of the individual pedicellaria as would doubtless be the case if they were independent. But behavior with the mere object of self-preservation, comparable to the fleeing away of an entire animal, is found in pedicellariae under certain desperate conditions.

The behavior of the pedicellariae of the sea-urchin has been studied with great thoroughness by von Uexküll (1899), and his observations will be of interest for comparison with what we find in the starfish. In his paper von Uexküll gives an extended history of the development of our knowledge of the pedicellariae in both the sea urchins and the starfish, and of the various theories that have been held as to their nature and function; it will therefore be unnecessary to give such an account here. No detailed study of the physiology of the pedicellariae of the starfish has been published,, though, as we have seen, Cuénot describes briefly their action in protecting the gills from small worms.

Kinds of Pedicellariae.—The starfish under consideration (*Asterias forreri*) has two kinds of pedicellariae, differing much from each other, together with a third kind that is in some respects intermediate between the two others. By far the most numerous are the pedicellariae already described (fig. 1), which are grouped in the rosettes or rings surrounding the spines. These have the typical structure of the common starfish pedicellariae. The two jaws form a cross, like a pair of pliers, with a third piece between them, on which they move as on a pivot.

Among these are scattered a few enormous pedicellariae, nearly as large as the spines of the starfish. These are not grouped, but usually stand solitary, rising from the surface of the body among the spines; not infrequently two or three are placed close together. They are formed on the well-known type of a basal piece, on which rest the two jaws, not crossing, but opposed throughout their length; they may, therefore, be compared in structure to a pair of sheep shears. The number and distribution of these large pedicellariae vary in different individuals. Some have hardly one; others bear a dozen or

more. They are likely to be found chiefly in the region of the junction of the rays with the disk, though they may occur elsewhere. After the eye has become accustomed to studying with the lens the numerous minute pedicellariae surrounding the spines, it is almost startling to come suddenly upon one of these monsters, often gaping widely so as to remind one of the hippopotamus in the circus posters, and showing even to the naked eye a formidable set of teeth. Their behavior is different in many ways from that of the other pedicellariae, so that we shall take it up separately.

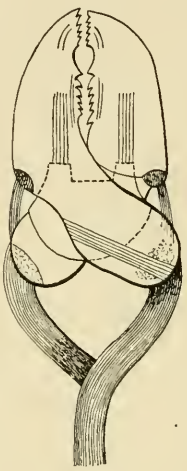


Fig. 3.—Pedicellaria, showing the three pieces of which it is composed, and the muscles by which it is opened and closed. After von Uexküll.

In addition to these two kinds, there are in some individuals a few examples of a third sort of pedicellariae. These are little larger than the ordinary type, but have the same structure as the large pedicellariae just described. They are usually found scattered near the madreporic plate and in the region of the angle between the rays. We shall not deal separately with their behavior.

Action System.—The main actions of the pedicellariae are their movements of attack, and of withdrawal. In the former they rise to the top of the spines, open, seize an object with which they may come in contact, and hold to it. Under certain other conditions they withdraw and close. We wish to determine just

why sometimes one of these movements takes place, sometimes another, and the rules followed in the actions. We will take up each act or set of acts separately.

The Attack.—What causes the rosettes of pedicellariae surrounding the spines to rise to the attack? This is usually caused, as we have seen, by some creature which gets among the gills and spines, and disturbs them. But there are many conditions on which it depends.

As a rule the pedicellariae do not rise unless there are repeated stimuli. If an organism touches the starfish but once, or if we thrust a bristle against the gills or against any of the structures on the upper surface of the starfish, there is either no response to the first touch or merely a slight movement of the pedicellariae. At the second the rosettes may show slight indications of rising, and if the stimulation is again repeated they suddenly push up to the top of the spine. Thus the first effect of a stimulus is to throw the rosettes into a certain preparatory physiological state. While in this state a repetition of the stimulus causes them to rise.

In rare cases the rosettes are already in this irritated condition, owing to the general bodily condition of the animal, so that they rise to the attack at the first touch. This will be spoken of later.

Usually therefore, objects which come against the starfish and remain quiet are not attacked by the pedicellariae. If we press steadily on the tip of one of the spines, the rosettes do not rise, though if we draw a hard body across the tip of the spine, or if we strike it several times, they rise to the attack. If we drop sand on the surface of the starfish, the grains are not seized by the pedicellariae, even though the sand may cover a number of the delicate gills. Any fine flocculent material on the surface of the animal is left undisturbed,—though we may cause the pedicellariae to seize it by disturbing them with a needle. Any small animal in contact with the starfish is safe so long as it remains perfectly quiet. Of course, this rarely happens, and as soon as the animal begins to stir about, it is seized. If a small object which has been seized by one of the pedicellariae *pulls*, this causes all the pedicellariae of the rosette to rise. Thus the pedi-

cellariae are so constituted as to attack, under natural conditions, only *living* creatures; inanimate objects, keeping quiet, are left alone.

The attack of the pedicellariae may be brought on by stimuli on any part of the dorsal surface of the starfish. The part touched may be the bare tip of the spine, its fleshy sides, the rosettes themselves, the large or small pedicellariae, or the gills; the result is to cause the neighboring rosettes to attack.

Varied Reactions.—The attack of the rosettes is not a mere stereotyped reaction, bound always to occur completely and in the same way in any given rosette. On the contrary, parts of a rosette may react separately, or in different ways, and there is an active seeking out of the stimulating object. This is shown in a striking way in the following experiment. If after a rosette has risen to the top of the spine, and all the pedicellariae are reaching upward with gaping jaws, we stimulate with a needle one side of the base of the spine, below the rosette, then we find that this side of the rosette curves over and bends down, directing the pedicellariae downward, so that they are likely to seize the offending object. This does not resemble at all a mere retraction, an undoing of the original extension, but is an active additional reaction. In a similar way different parts of the rosette often reach out in various directions, depending on their relation to the region stimulated; or individual pedicellariae bend over to that point on the rosette where a localized stimulus is given. We have already seen, in our general account, that the spines bend with the entire rosette toward a spot on the body that is disturbed; they may thus bend in any direction. The large solitary pedicellariae likewise bend toward a stimulated spot, though for these the stimulus must be near. The large pedicellariae usually do not bend toward a stimulated spot that is distant more than their own length.

When there is a general stimulation of the starfish as a whole, the spines and pedicellariae often wave about, the jaws snapping repeatedly, in this way much increasing the chances of finding and seizing the cause of the disturbance. Thus a separate external stimulus is not necessary for each opening or closing of a pedicellaria; there are changing internal states which have the same effect.

Effects of Different Stimuli.—Not all effective stimuli cause the same response in the rosettes. Mechanical stimuli of sufficient intensity, if repeated, always cause the rosettes to attack. Cutting or crushing a part of the body causes the rosettes of the entire surrounding region to attack fiercely. If for example we thrust a needle through the body wall, the surrounding rosettes rise and bend over toward the injured spot. Very light mechanical stimuli, on the other hand, often produce no effect, even if repeated. Thus, certain small soft nudibranch mollusks (species of *Chromodoris*) were seen at times to creep over the surface of the starfish without causing the pedicellariae to rise. But the larger specimens, causing slightly greater pressure, were usually attacked. A strong current of water injected against a small area often causes the pedicellariae to rise; weaker currents do not.

The effects of chemical stimuli differ with different substances. Fresh water brought into contact with the body surface produces only a languid response; the rosettes may slowly rise part way, and a few of the pedicellariae open. Often there is no response to this. Acids cause the rosettes to contract strongly, shrinking away and hiding the pedicellariae. In the case of picric acid the pedicellariae opened, though the rosettes shrank away as far as possible. Crystalized salt from sea-water caused strong contraction and closure. Alkalies (KOH, NaOH) when weak cause the rosettes to extend and the pedicellariae to open; when strong they cause contraction and closing. Potassium bichromate and various other chemicals have the same effect. With potassium bichromate used in a rather weak solution, there is for a time a maximal extension of the rosettes in all the affected region. No other form of stimulation produced so strongly marked and unvarying an effect. About two minutes after the action of the chemical had ceased, the rosettes began to retract. *After* this chemical stimulation there is a much readier response to mechanical stimuli; a single touch with a needle or bristle now brings up the surrounding rosettes in haste. Methyline blue injected into the cavity of a ray through a small opening caused the rosettes to rise over the entire surface of the region affected, though injected sea water did not have this effect.

Some responses to chemicals are food reactions rather than defensive movements. This is the case with the juice of crab meat. If a little of this juice, or a piece of the crab meat, is brought near the dorsal surface of the starfish, the rosettes rise, the pedicellariae open, and if possible seize the meat. The latter is then carried to the mouth, in the way that will be described in our account of the food reactions.

Perhaps the surest way to cause the rosettes to attack is to let another starfish brush against the specimen under observation; there is usually a prompt rising of the defensive organs over a large area. The touch of a single tube foot of another individual often causes extensive rising of the pedicellariae; the animal bristles up like a cat. Even when an individual draws one of its own rays across another there is a general rising of the rosettes. Contact with almost any other animal has a similar effect. In these cases there is perhaps a combination of chemical and mechanical stimulation.

In many specimens, if the animal is seized and turned on its back, or is otherwise maltreated, there is a simultaneous attack by all the rosettes; they rise and the pedicellariae open. Whether this occurs or not depends partly on the general physiological condition of the individual. Starfish which have been weakened through a long stay in the laboratory tanks commonly do not react in this way, while those freshly brought in from the sea are much more likely to do so. In general, I found that large, old specimens are much more likely to respond by a general bristling upon slight provocation than are younger ones. There is much individual difference in this matter. Working for some time continuously with a number of individuals, one gets an impression as of the existence of mild-tempered starfish and of exceedingly ill-tempered ones. A certain large starfish *H*, used in my experiments on habit formation described later, belonged to the latter class; whenever touched, its rosettes all rose savagely.

Opening, Closing and Grasping.—In the retracted rosettes the pedicellariae are, under ordinary conditions, closed. If now a small animal or other object comes against one of these resting pedicellariae, the latter does not react at all. Before it will snap,

it must be roused and caused to open, the rosette as a rule beginning to rise at the same time. In some cases the pedicellariae will open before the rosette rises, but this is not usual. If we try stroking lightly the outer surface of a pedicellaria in a rosette that has not risen, taking pains not to touch anything else, often the only effect is to cause the pedicellaria to retract, drawing downward without opening, so that it may almost bury itself in the fleshy mass of the rosette. If we repeat the light taps a number of times, the pedicellaria may now turn a little to one side, then, while thus contracted, open a little and snap together again, —all without affecting any of the surrounding pedicellariae. Next it often rises again to the usual level, and opens its jaws. If anything comes between the jaws, they snap and hold tightly. If the taps on the back of the pedicellaria are *very* light, usually there is no reaction until twelve to twenty taps have been given. If they are a little stronger, or if the pedicellaria is more sensitive, four or five taps are enough to cause it to behave in the way just described.

But usually it is not easy to get a single pedicellaria to react alone. The stimulus is evidently transmitted through the fleshy substance of the rosette, so that after four or five taps the immediately contiguous pedicellariae begin to open, while the one stimulated still remains closed. A little later it opens also, and that portion of the rosette usually begins to rise.

As we have seen, picric acid causes the pedicellariae to open, though the rosette contracts strongly.

While thus the opening of the pedicellariae may occur before the rising of the rosettes, this is usually not the case. As a rule the rosettes begin to rise, and this is then accompanied or followed by the opening of the pedicellariae. But the two actions are not necessarily bound together: the rising of the rosettes may occur without the opening of the jaws. There is often great variation among neighboring rosettes on the same starfish in this respect. When a certain spot is jabbed with a needle, some of the surrounding rosettes merely rise, the pedicellariae not opening till there is a new stimulus, while in other rosettes the pedicellariae open even before the rosettes rise, and in other cases the rising of the rosettes is succeeded by the opening of the pedi-

cellariae without farther stimulation. These differences are doubtless due to different physiological states in the different rosettes, resulting from different past histories. They seem not due to different ages of the rosettes, since contiguous rosettes at the same level of the ray may show these differences.

Even in the same rosette, after it has risen, some of the pedicellariae may be open, while others remain closed.

Let us suppose that a rosette has risen, but that the jaws have not opened, as we often find to be the case. What will now cause the pedicellariae to open?

This is usually brought about by rubbing or jabbing the rosette; usually all of its pedicellariae open at once, both those directly struck, and those not touched. Any stimulus that causes the rosettes to rise will, when repeated, cause the pedicellariae to open. If the rising has been caused by a chemical stimulus, a light mechanical stimulus following the chemical causes the opening.

If in an extended rosette in which the pedicellariae are still closed we try stimulating the individual pedicellaria by touching its outer surface with a fine hair or bristle, it is usually not possible to get it to open alone. As a rule the immediately contiguous pedicellariae open first, the stimulation evidently being transmitted through the underlying fleshy mass. The pedicellaria directly stimulated then opens a moment later. In rare cases, by stimulating very lightly the *outer* surface of a single pedicellaria, it alone may be induced to open.

The large solitary pedicellariae are usually readily induced to open by lightly touching several times the outer surface. The jaws then gap widely and remain open for sime time:—often for as much as five minutes. When several of these large pedicellariae are near together, a stimulus on the outer surface of one causes its neighbors to open simultaneously with it. A stimulus on the gills or the body surface near the large pedicellariae usually causes them to open and bend toward the spot stimulated. But sometimes they merely bend over toward the spot, and wait for a new stimulus before opening. A large pedicellaria may likewise be caused to open by rubbing the side of its stalk, or even by thrusting a fine-pointed glass rod into the angle between the lower parts of the two jaws.

The effect of a stimulus when repeated often differs from its first effect. Thus, in many cases I observed that when the gills near one of the large pedicellariae was struck with a fine rod, the pedicellaria opened slightly, in a weak sort of a way, then closed again. Now the gills were struck again as before; the pedicellaria did not open, nor would it open in response to further repetitions of the stimulation. Again, often the pedicellariae will not open in response to one or even several stimuli, but if the stimuli continue, the opening may finally occur. The following illustrates these variations: Two large pedicellariae, which we may call A and B, stood close together. Each was rubbed lightly on the back of the right jaw, near the tip. Each at once opened about one-eighth of the full amount, remained thus one or two seconds, then closed. Now A was rubbed again in the same way; it did not open, but instead bent over toward the side stroked. The stimuli were now repeated five times in succession without response, till at the fifth stroke the jaws opened much more widely than before.

Waiting for two minutes after the jaws of *A* had again closed, the stimulus was repeated. To the first stroke the pedicellaria responded by opening half way; then after closing it did not respond to the next three strokes, but the fifth again caused it to open slightly.

In the case of *B,* the first stimulus on the right jaw caused slight opening. The next three, on the same spot, had no effect. Now the *left* jaw was similarly stimulated in the corresponding spot; the pedicellaria at once opened.

It is evident that the motor apparatus of the pedicellaria is in a state of somewhat uncertain equilibrium, varying at different instants, and depending largely on the recent history of the pedicellaria. Its response depends upon its precise state at the moment of stimulation.

Opening of the jaws does not always require a definite stimulus. Often, if the jaws, at being opened, are stimulated to close, they at once open again if their first closure did not result in seizing an object. They may of themselves snap repeatedly,—opening and closing without any further stimulus than the preceding action,—the opening evidently predisposing them to

close, and the closing to open. This occurs usually only under the influence of some general stimulus which has roused the pedicellaria,—bringing on a condition of unstable equilibrium.

If the large pedicellariae (or the region about them) are repeatedly and strongly struck and abused, they close up tightly and remain closed. Now the surrounding rosettes of small pedicellariae rise and open their jaws. Thus the large pedicellariae open in response to a weaker stimulus than do the small ones, and withdraw when the stimulation becomes intense enough to engage the attention of the latter. Von Uexküll found analogous differences among the different classes of pedicellariae in the sea urchin. A chemical stimulus causes the "ophicephalous" pedicellariae and the spines in the sea urchin to shrink away, while the strong poisonous pedicellariae advance to the attack.

Closing.—Most stimuli which cause the rosettes to withdraw and contract likewise cause the pedicellariae to close. But, as we have already seen, this is not invariably the case,—picric acid sometimes causing the rosettes to contract strongly, while the pedicellariae open. This varies much in different cases. Picric acid always causes complete contraction of the rosettes, but this is sometimes accompanied by closure of all the pedicellariae, sometimes by closure of part while part remains open, sometimes by the opening of all the pedicellariae of the rosette.

If the pedicellariae have been caused to close by a chemical stimulus, they later refuse for some time to open even under the usual stimuli that cause opening. If one touches the retracted rosettes repeatedly, in the way that commonly causes them to extend, they remain obstinately contracted, while the pedicellariae remain closed.

The closing of the pedicellariae when objects are seized is usually brought about by a touch on the inner surface of the jaws. The latter then snap quickly, seizing the object which touched them. This action is best studied in the large pedicellariae, where the jaws are so extensive that their inner surface can be surveyed and the effect of stimuli in different regions determined. The inner surface is divided by a sharp transverse ridge into two parts; below this ridge the surface is hollowed. Touching the inner surface of the pedicellariae above the ridge

usually causes the jaws to snap together, while a touch in the throat below the ridge has no effect, even though the touch is roughly given. Often, also, a touch on the inner surface of the jaws at the very edge, on the teeth, does not cause closure.

The effects of stimuli on the inner surface are not invariable, but depend, like all of the reactions of the pedicellariae, on various conditions. Thus, if we cause the pedicellaria to open by a stroke on the outside of its jaws, then, while it is opening, we stimulate the inner surface in the way that usually causes closure, we find that this has now no effect; the jaws continue to open. When once a certain action is set in progress, this proceeds with something like inertia, so that it is not easily stopped. We shall meet with many examples of this in the behavior of the starfish. The phenomena just described are evidently analogous to the refractory period seen in muscles of higher animals.

In the small pedicellariae, as in the large ones, the usual stimulus to closure is the contact of some object with the internal surface of the jaws, resulting in the seizure of that object.

But in both the large and the small pedicellariae, closure often results from internal changes. When a general stimulus is given to the starfish as a whole, often the rosettes rise, the pedicellariae reach out and snap frequently, opening and closing several times without change in the external conditions. The large solitary pedicellariae after bending over toward a stimulated spot often snap repeatedly. The performance of one action results in so changing the internal conditions as to cause the performance of another. But in the pedicellariae of the rosettes this occurs only in certain general physiological states of "excitement," due to a preceding marked general stimulus.

In such cases, as soon as the pedicellaria snaps upon any object, so as to hold it, the jaws do not open again, but hold for a time. If while the jaws are holding, this pedicellaria or the neighboring region is stimulated in the way that usually causes opening, the pedicellaria with an object in its jaws usually neither extends nor opens, though all of its fellows rise fiercely to the attack and open widely. If this region is abused roughly, the jaws only close the more tightly. But there are some curious variations in this. Thus, in one case a pedicellaria had held a

short piece of hair for about half an hour. The rosette to which it belonged was jammed with a needle, whereupon this pedicellaria opened for an instant, so that the hair could have been withdrawn, then snapped tightly again, and thereafter held the hair in a vise-like grip, in spite of repeated violent stimulations of the rosette. Meanwhile, the other pedicellariae of this rosette were open and widely extended.

It sometimes happens that the living animal which has been seized pulls violently, stretching the stalk of the pedicellaria, and finally jerking itself from between the jaws. The latter then snap together, while the pedicellaria retracts strongly. Now this pedicellaria remains for a long time quite unresponsive to stimuli; it does not extend nor open, even though all its neighbors do so.

Length of time that the jaws remain open.—After the large solitary pedicellariae have been stimulated to open, they sometimes remain opened five minutes or more. Often, however, the large pedicellaria remains open but a minute or two, or even but an instant, snapping shut quickly after it has opened. It is not rare to find some of these remaining widely open in an apparently undisturbed starfish, though all the small pedicellariae are tightly closed. When this is the case, then jarring or disturbing the animal often causes the jaws to close, though the same stimuli, under other conditions, cause the jaws to open. The small pedicellariae usually remain open after stimulation for but one or two minutes. But in all of the pedicellariae this depends largely on the intensity of the stimulation. A weak stimulus causes but a momentary opening, a stronger or repeated stimulus induces the pedicellariae to remain open for some time. Very intense stimulation often causes alternate opening and closing, the pedicellariae snapping in various directions, as if reaching for the disturbing object.

Time of holding.—(*a*) *Pedicellariae of the rosettes.* After the pedicellariae have seized an object there is extraordinary variation in different cases as to the length of time it is held. In general it may be said that the small pedicellariae of the rosettes usually hold to any object that pulls or moves, for an indefinite period. I have repeatedly kept note of individual

pedicellariae that held to small crabs for an hour or more. It is very common for a small crustacean to be held immobile on the back of a starfish for forty-eight hours or more, and there is no indication that the pedicellariae change off or take turns in holding; apparently the same pedicellariae hold for the entire period.

Living animals seized by the pedicellariae usually try to pull away, and the small pedicellariae are so constructed that the pulling tends to make them hold the more strongly. The two jaws are crossed like the blades of a pair of scissors, and to the end of each is attached a muscular strand. These two strands come together and extend straight down the stalk of the pedicellaria (fig. 3). When the pedicellaria is pulled, so as to stretch the stalk, these two strands necessarily tend to hold the two jaws more tightly together. The stalk is extremely short—hardly noticeable, indeed,—under usual conditions; it is shorter than the pedicellaria itself. But it may stretch to many times the length of the pedicellaria. When the object seized pulls too strongly it will usually slip out of the jaws before the stalk breaks. Thus the pedicellariae are rarely pulled off, though this sometimes happens. This pulling of objects away from the pedicellaria is a common episode in the capture of food. After a stretched pedicellaria has been released, it contracts strongly, and remains contracted, not opening in response to stimulation for a long time.

But the long continued holding of the pedicellariae is not due alone to the pulling, with its attendant stretching of the muscle, as might perhaps be supposed. Minute lifeless objects are often held for long periods. In one case a single pedicellaria was observed holding a minute lifeless spine for thirty-four minutes; in another a minute appendage from a crustacean was held while under observation for forty-two minutes; in another a bristle from a brush was held for twenty-one minutes. How much longer before and after the period of observation these objects were held I do not know. Many similar cases were observed. As we have before noted, while thus holding an object, the pedicellariae do not, as a rule, open when stimulated in a way that causes the free pedicellariae to open.

On the other hand, minute objects are often held for but a

moment. Fine flocculent material is not seized at all unless the pedicellariae are stirred up by stimulating them with a needle, or the like, and it is held but a few seconds. Possibly pressure on the internal surface of the jaws is necessary to cause the pedicellariae to hold. Yet a tube foot from another starfish was held tightly till it was broken off in pulling away. And small hard objects are sometimes released a moment or two after seizure, just as soft ones are.

It is clear that the holding by the pedicellariae depends on many factors, doubtless to a large degree internal, so that the precise behavior of a given individual pedicellaria can not well be predicted.

(*b*) *The large solitary pedicellariae* are usually less inclined to hold objects a long time. Usually they release in a few moments even hard objects, and notwithstanding the fact that they stir or pull. But there is much variation in different pedicellariae. Thus, two of these large pedicellariae were standing near together on the same starfish. A small, soft insect larva was dropped into the open jaws of one of these. It at once closed on the larva, then opened again, and repeated this several times, finally remaining open. Its neighbor was given a similar larva; it thereupon closed and held it tightly for two minutes, when the larva managed to pull away. The leg of a large blow-fly was placed between the jaws of the first of these two pedicellariae. It was at once seized, then at once released, though the fly struggled and pulled. Then the same leg was placed between the jaws of the second pedicellaria. It at once closed and held on stoutly for *three hours and forty minutes*, the fly struggling and pulling for a long time. I then broke off the observation. It is therefore evident that sometimes the large pedicellariae may hold on indefinitely, though this is not so common as with the small ones.

In thus holding for long periods, the pedicellariae of this starfish appear to differ from those of the sea urchins. Von Uexküll reports that the latter hold an object seized for only about two minutes.

Seizing parts of the Starfish.—In another way the pedicellariae of the starfish differ from those of the sea urchin, as

described by v. Uexküll. The pedicellariae of the sea urchin refuse to seize or hold each other, or other parts of their own body, or of other individuals of the same species. If through accident a pedicellaria snaps upon a part of its body it at once opens. Von Uexküll calls this properly "autodermophilie," and believes that it is due to the presence in the tissues of a substance which paralyzes the closing muscles (1899, p. 376); this substance he calls *autodermin*.

In this starfish we find nothing of this kind. The pedicellariae seize and hold each other apparently as readily as any other object. One often sees cases like the following: Two rays of a starfish were lying side by side, and two pedicellariae of each ray had interlocked jaws with the two of the other ray and were holding on, the stalks stretched far. As the two rays moved, the stalks of the four pedicellariae stretched farther or contracted like India rubber, always remaining taut. While under observation these pedicellariae retained their hold on each other for thirteen and one-half minutes.

Pedicellariae of neighboring rosettes on the same ray frequently seize and hold one another. They sometimes hold for a long time, even when there is no tension by either. The pedicellariae of one starfish may seize any part of another. I have seen a tube foot of one specimen torn off as a result of being held by a pedicellaria of another.

In certain experiments the body of a starfish was cut into large and small pieces. When one piece was brought into contact with the surface of another, the pedicellariae of the latter seized any part which they could reach, setting their jaws into the bony framework, the connective tissue, gills, or other tissues, and holding them. I saw pieces thus held for more than five minutes by pedicellariae of the same individual; how much longer I did not observe.

Independent Reactions and Transmission of Stimuli.—Von Uexküll has brought forth clearly in the sea urchin the power of independent reaction on the part of the pedicellariae. Each may behave in the usual way when isolated on a small separated piece of the shell of the animal. A somewhat similar condition of affairs is found in the starfish. If a small piece of the body

wall, bearing but a single spine, is cut from the remainder, the rosette rises to the top and the pedicellariae open,—this reaction being due to the stimulus of the cut. Now the pedicellariae seize any small object which touches them. Such a piece suspended itself for about a minute by the pedicellariae from the hairs on the back of my hand.

On the other hand, the large solitary pedicellariae could not be induced to bend over or to open, when isolated on a small piece of the starfish.

Even in the case of the pedicellariae of the rosettes, of course it will not do to conclude from the possibility of reaction to independent stimuli, that the reactions of each rosette are always due to external stimuli directly affecting that rosette. On the contrary, nothing is clearer than the fact that the stimulus causing the attack is usually transmitted from some other part of the body. The pedicellariae of the rosettes may respond to stimuli far away. A prick on the tip of a ray or the mere touch of a single tube foot from another starfish, often causes all of the rosettes of that ray, and perhaps of one or two of the contiguous rays to rise to the attack. Indeed, a strong stimulation in one region often causes all the rosettes of the starfish to rise, the creature bristling up like an angry cat.

The large solitary pedicellariae likewise respond to stimuli at a distance, though, as we have seen, at but a short distance. When two of these are near together, a touch on the outer surface of one commonly causes both to open simultaneously. Sometimes the one touched opens first, then the other. But if one is now stimulated to close by touching the inner surface of the jaw, the other does *not* close. Thus the stimulus to open is transmitted, while that to close is not.

How is the stimulus for the pedicellariae transmitted to a distance? Von Uexküll has shown that in the sea urchin this transmission need not pass through the radial nerves, and the same is true for the starfish. If we cut through the radial nerve, or the entire ventral half of the ray, the stimulus is still transmitted from one side of the cut to the other. A prick at the tip of this ray may cause the pedicellariae of other rays to rise, or a stimulus on another ray may cause the rosettes of the cut ray to

rise. Cutting the nerve usually itself acts as a strong stimulus to the rosettes of the region nearby, causing them all to rise and remain extended for some time. Soon after these rosettes near the cut have subsided, a stimulus on some other part of the body caused them to rise quickly; the cut has evidently left them in a condition predisposing to ready reaction. If the nerve is cut in the middle of a ray the rosettes of the distal half seem specially affected, remaining extended for some minutes.

If the dorsal body wall of a ray is isolated, so that it contains no part of the radial nerve, stimuli on any part of this piece are transmitted to other parts, causing all the pedicellariae to rise. The transmission is not so complete soon after the piece has been cut out, as later.

Altogether, it is probable that the transmission of stimuli for the pedicellariae takes place in the starfish largely through the nerve nets of the body wall, as von Uexküll sets forth for the sea urchin.

It is important not to think of the transmission of the impulse to rise as taking place in too simple a manner, or as determined by purely anatomical arrangements. What distant rosettes shall rise when a given point on the body is stimulated depends more on the recent history of the different parts than on the permanent anatomical connections. This is shown by experiments of the following character. In a quiet starfish a certain region (say, the tip of the arm *a*) is stimulated, till the rosettes of that region rise to the attack. These are allowed to subside, then a few moments later another part of the body, at a distance (say, the tip of the arm *d*) is stimulated in the same way. Now its pedicellariae rise, and *also the pedicellariae of the part stimulated before* (near the tip of the arm *a*), though the pedicellariae of the intervening region do not rise.

Thus the reaction of the rosettes in a certain region leaves them for a time in a changed physiological state, so that they are readier to react to impulses coming from a distance than are even the rosettes nearer the point stimulated. The effective transmission of the stimulus from the arm *d* to the arm *a* is not due to any closer nervous connection between these arms than between *d* and the others. It is due only to the greater readiness of *a* to

react, owing to a transient physiological state impressed upon it by its recent history.

A peculiarity of transmission less easy to interpret was shown in the following observations. A starfish was lying in an extended position, the arms *a* and *c* of the bivium projecting in one direction, as in fig. 4. Thus the animal was temporarily bilaterally symmetrical, with long axis passing through the arm *c* and between *a* and *c*. The right and left sides of this bilateral organism are formed by the outer sides of *c-d* and *a-b*. Another starfish brushed along the outer side of *e*. At once the rosettes of

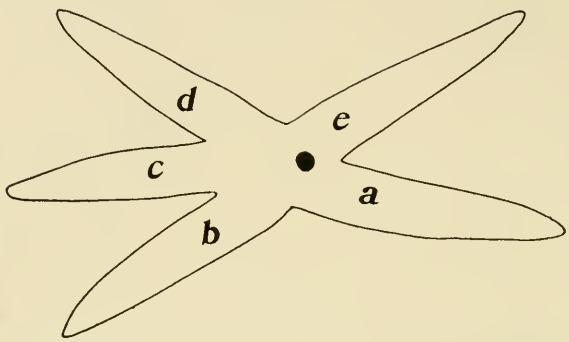


Fig. 4.—Starfish extended in such a way as to take a bilateral form. See text.

that region rose to the attack, and also those of the exposed outer sides of *a*, *b* and *d*—that is, the rosettes of the entire exposed outer sides of the rays—while the rosettes of the protected ray *c* did not respond, nor did those along the protected *inner* sides of the other four rays. A repetition of the stimulus after subsidence of the rosettes brought about the same peculiar response. I had no opportunity to study this effect on other specimens.

Influences determining Variation and Modification of Reactions in the Pedicellariae.—As we have seen, the behavior of the pedicellariae under given external stimuli is by no means stereotyped. It depends upon many different conditions, and among these determining conditions are varying internal states of the organism depending largely upon its past history. It will be worth while to summarize here, at the cost of some repetition, the

different modifying factors thus far mentioned. The readiness to react, the nature of the reaction, and the transmission of stimulation,—all these depend in the varying internal physiological conditions of the organisms. We will take up separately the different actions which the pedicellariae perform, mentioning the various factors determining each.

I. The rising of the rosettes to the attack. This has been shown to depend on:

1. Foregoing preparatory mechanical stimuli. The rosettes do not rise in response to the first, nor completely even to the second or third stimulus. We can distinguish thus a resting condition and a series of intermediate preparatory conditions, before the rosette reaches the active condition in which it responds to a weak mechanical stimulus.

2. Preparatory chemical stimuli induce a condition in which the rosettes rise more readily under the usual mechanical stimuli.

3. Foregoing chemical stimuli of a certain character have the opposite effect, inducing a physiological state in which the rosette refuses to attack under the stimuli that usually cause it to do so.

4. Cutting the radial nerve leaves the rosettes in such a state that they attack more readily than usual in response to any mechanical stimulation, either close by or at a distance.

5. Weakness in the animal, from long confinement, causes the rosettes to attack less readily in response to stimuli at a distance from them.

6. The rising of the rosettes in a certain region leaves them after subsidence in such a state that they react more readily to stimuli in a distant part of the body than do even rosettes nearer the source of stimulation.

7. There are general differences characteristic of individual starfish. In some all the rosettes attack readily; in others the attack is not easily brought about.

II.—The opening of the pedicellariae. This depends on the following factors:

1. Homogeneous preparatory stimuli. In a series of similar stimuli, several are usually required before the pedicellariae respond by opening. There are several variations to be noted here:

(*a*) Sometimes there is no response to the first stimulus; but this and one or two succeeding ones cause a gradual change in physiological state, so that the pedicellariae later open.

(*b*) Sometimes the first stimulus causes retraction and closing, while later ones of the same kind produce extension and opening.

(*c*) Sometimes (in the large pedicellariae) the first stimulus causes slight momentary opening; the next two or three have no visible effect; the next, pronounced opening.

2. Chemical stimuli of a certain character cause the pedicellariae to open later more readily under mechanical stimuli.

3. Chemical stimuli of a certain character cause later refusal to open under the usual mechanical stimulation.

4. Holding some object causes the pedicellariae to refuse to open under the usual mechanical stimuli.

5. Long holding an object causes the pedicellaria, after release, to refuse to open under the ordinary stimuli.

6. Repeated intense mechanical stimuli cause the large pedicellariae to refuse to open under the usual stimuli.

7. After closing the pedicellariae often open and again close spontaneously, "snapping." The foregoing action furnishes the condition for the succeeding one.

There are similar variations, as we have seen in detail, in the time that objects are held and in the order of the different actions—the opening sometimes preceding the rising, sometimes following it, etc.

Altogether, it is clear that the reactions of the pedicellariae are determined by a multiplicity of factors, giving rise to much variation in the responses under given present external conditions.

Capture of Food.

We have seen the action of the pedicellariae in assisting the process of getting oxygen. Let us now see how the starfish provides the other materials for keeping the processes of metabolism in progress. Besides oxygen, it must have a supply of proteids and of other complicated chemical compounds, or the processes making up life will cease.

Convenient bundles of precisely these necessary chemicals are found in the crabs, mollusks and other animals that inhabit the rocks of the sea-shore. We find the starfish furnished with an outfit of structures and movements by which such bundles of chemicals are incorporated in its own body and their contained energy is diverted into the channels of its own processes.

The pedicellariae, as we have seen, often capture and hold indefinitely the animals which are so unfortunate as to come against the starfish. Sometimes such animals are merely held till they die, and the store of food they might supply is wasted. But usually, if the animal is not too small, the starfish proceeds to devour the captured prey. Indeed, as we shall see, it is clear that one of the main uses of the pedicellariae is to capture food.

Let us examine a typical case of the capture of food. Five starfish were placed in a large glass vessel with flat bottom, and into this same vessel were placed nine small crabs. The crabs scuttle quickly to a hiding place on or behind the starfish, but are at once seized by the pedicellariae of the rosettes. Discovering their mistake, the crabs struggle to get away, and fight savagely, pinching the starfish with their claws and pulling off bunches of pedicellariae. The largest crab, nearly an inch in diameter, manages to escape, but the others are held on the upper surface of the starfish.

Now in several of the starfish we see the tube feet with their suckers pushing up from beneath and feeling about toward the captured crabs. They feel about for two or three minutes, and a few of the suckers manage to attach themselves. But by this time the crabs have become quiet, and the tube feet are withdrawn, leaving the crabs attached and immobile on the upper surface of the starfish. Thus they remained for a long time on most of the starfish.

But after about ten minutes one of the starfish, that had captured, on the sides of two adjacent rays, three small crabs, each about one-half inch across, began to take more active measures toward feeding on them. The three crabs were on the facing sides of the two rays,—thus in one of the interspaces between the rays. The starfish began to bend these two rays toward each other, so as to crowd the crabs together, and at the same time the

rays bent downward, so as to bring the crabs toward the under side of the disk of the starfish. The disk itself began to rise, so as to make it possible for the two rays to be doubled beneath it; the crabs were thus carried to its under surface. Up to this point the tube feet had played no part, the crabs being held by the pedicellariae and carried toward the mouth by the bending of the rays. Now the tube feet are sent out, especially from the disk region, and the suckers are applied to the crabs. The disk is slowly raised as much as an inch from the bottom; and two of the rays are bent directly under, so that their ventral surfaces are applied to the mouth. Thus one of the crabs is placed against the mouth and held there. But this crab now makes violent efforts to escape, and nearly succeeds. It is caught again by the tube feet and pedicellariae, while a third ray now bends under the disk and helps push the crab to the mouth. The crab is this time securely held, almost covered with tube feet. The three rays straighten, and the starfish flattens down against the glass, with the crab against its mouth. The soft lobes of the stomach come out through the mouth, after the horrid fashion of the starfish, apply themselves to the living crab, and proceed to digest him.

Meanwhile the other two crabs have been carried to the under surface of the starfish also, and are there held quiet by the tube feet, till such time as the starfish shall be ready to devour them. One of them seems completely conquered, and remains still. But the larger one makes a violent effort to escape while the starfish is digesting his companion; he manages to pull away to the tip of one of the rays. The starfish follows in that direction, carrying the other two crabs, and seizes the unruly crab anew with its tube feet. But the crab has managed to free its great pincers, and with these it savagely cuts off the tube feet that are holding it, and flees. In the melée a considerable number of legs have been pulled off the different crabs; four of these legs are now held by the tube feet against the lower surface of the starfish, until such time as it shall be ready to devour them.

The bending of the rays under the disk required but about five minutes, but it was nearly half an hour from the beginning of the fray before one of the crabs was applied closely to the mouth,

—and even after this, this crab nearly escaped, and it took about ten minutes to get it back into position again. The crab is held partly enveloped by the lobes of the stomach for some hours, during which time its soft parts are digested and absorbed; the empty shell is then released.

Many other animals fall victims to the starfish. In its natural surroundings its chief food is a small gasteropod which is very abundant on the rocks where the starfish lives. These are captured, of course, without any such struggle as that required to reduce the crabs to quiet. They are taken by the tube feet, turned over, and the opening of the shell applied to the mouth. The lobes of the stomach are pushed into the opening and the soft parts digested and absorbed, while the shell is quite covered with the tube feet that are holding it against the mouth. There seems to be little opportunity for this species of starfish to feed upon bivalves, as the common Atlantic coast starfish feeds on the oyster. This starfish usually does not keep its disk lifted high, and enclose the food between its rays, as is said to be done by the Atlantic starfish when feeding. It usually lifts its disk no higher than is necessary to get the food beneath it, and then usually flattens out as much as possible while feeding.

The flat, elongated mollusk *Chiton* is very abundant on the rocks where the starfish is found. *Chiton* usually remains pressed flat against the surface, its soft parts covered by its shell. It is then protected from the starfish. The starfish creeps over its surface, taking hold of its shell with its tube feet, as it would any part of the rock. But as long as the *Chiton* remains pressed to the rock, the starfish makes no effort to pull it off and devour it. But if an unlucky *Chiton* gets turned over, or its soft lower surface comes against the starfish, it is quickly seized by pedicellariae and tube feet, applied to the mouth, and its soft parts eaten.

Almost any animal matter seems acceptable food. They were often found in the aquarium devouring other species of starfish, from deep water. The latter are without pedicellariae or other effective weapons of defense, and fall a ready victim to the present species.

The starfish will even attempt to devour so spiny an object

as the sea urchin, as Prouho (1890) and v. Uexküll (1899) have observed with some of the Mediterranean starfish. I placed a small sea urchin about two and one-half centimeters in diameter, in the aquarium near a large starfish. The sea urchin was a specimen of *Strongylocentrotus purpuratus,* with long, stout spines. It soon came in contact with one side of a ray of the starfish, near its middle. The rosettes of pedicellariae at once rose to the attack all over this ray; they seized the spines and tube feet, and other parts of the sea urchin, wherever they could get hold. This ray and the one on the opposite side of the sea urchin now began to curve inward and toward each other, so as to surround the sea urchin and draw it close, while the disk of the starfish began to rise, preparatory to the reception of the prey at the mouth. Soon both rays of the starfish were against the sea urchin; all the pedicellariae were attacking it, and the tube feet of the two rays came forth and lay hold on the sea urchin. But the sea urchin is not without defensive weapons; indeed it is, of course, in many ways more strongly armed than the starfish. Besides its long, stout, sharp spines, it has large three-jawed pedicellariae, some of them poisonous, and each one suspended at the tip of a long rod. All of these weapons at once became active in defense. The spines bent over toward the regions seized by the starfish and pressed their sharp points against the latter; the starfish pedicellariae tried in vain to get a hold on the hard, round spines. The large pedicellariae of the sea urchin seized the attacking tube feet of the starfish and compelled them to withdraw. The pedicellariae of the two animals seized one another, interlocking jaws; some of those belonging to the sea urchin were thus pulled off. A spirited combat continued for about five minutes, the starfish being throughout the aggressor. But at the end of five minutes the starfish had had enough, and began to uncurl its rays and withdraw. It took about five minutes for the animals to become disengaged, though both were working to that end. They separated; the sea urchin was *not* eaten.

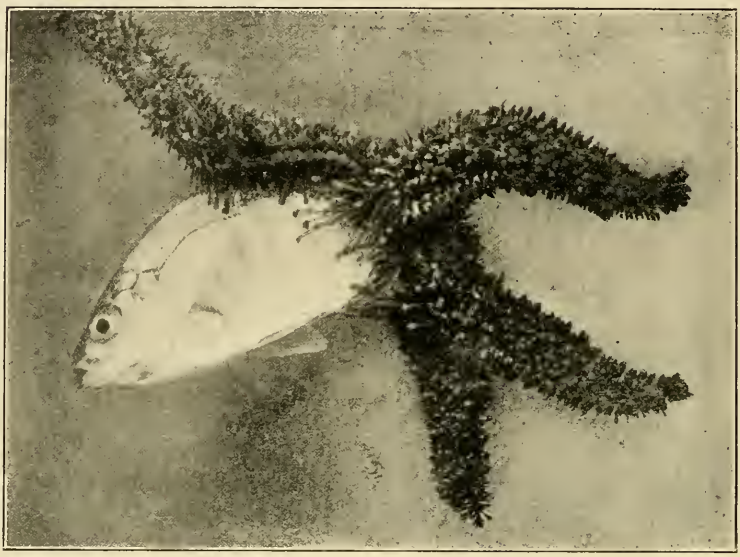
Five minutes later the sea urchin was again placed in contact with the starfish in the same place as before. The starfish at once began to withdraw, the pedicellariae rising defensively;

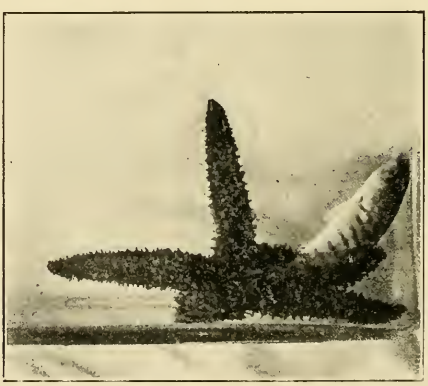
but there was no further attempt to capture the sea urchin for food.

In the aquarium the starfish frequently had better fortune in its attacks on certain animals that could hardly be expected to fall prey to it. It seems surprising that the starfish can capture such active, swift animals as fish. But in our tanks this often occurred. They captured and devoured fish having a length equal to the diameter of the starfish, from the tip of one ray to the tip of the opposite one. In one of our tanks a large number of starfish crawled about over the sides and bottom. At times numbers of fish of various sorts were kept in this tank, and it was soon found that the starfish were capturing them. The fish, swimming about, seemed to have no mistrust of the brown patches on the walls; when frightened they would even attempt to conceal themselves upon or against the starfish. The tail or a fin strikes in its motion the surface of the starfish. At once the rosettes rise, the pedicellariae open, and when the edge of tail or fin comes against them anew, it is seized by a hundred little jaws. Of course the fish gives a leap and attempts to pull away; the jaws hold, the fish struggles, and in struggling strikes other parts of its body against the starfish. Wherever there is a thin edge of fin, tail, or gills, the pedicellariae seize it, and the fish soon finds itself held tightly. Now the tube feet extend, the cruel suckers plant themselves over the smooth surface of the body, and the fish is transported to the mouth. In all cases observed it was the tail that was first brought to the mouth. The lobes of the stomach then come forth, press themselves against the tail and proceed to digest it, though the fish still makes at intervals violent efforts to escape. In the course of six or eight hours the posterior one-fourth of the body of the fish was usually quite digested, and the remainder of the fish was dropped. Figures 5 and 6 show photographs of the capture of fish by the starfish.

Certain interesting differences were observed among different fish as to the danger of capture by starfish. When there were placed in the starfish tank fish that in their normal existence spend their time swimming about in the open water, not coming against stones or other objects save when they attempt to hide

from actual danger, these were readily caught by the starfish. When these fish came in contact with the animals, their movements were strong, sudden, incautious, so that the pedicellariae were soon roused to attack. But the fish that in their normal existence live in rocky pools and under stones, resting much of the time against the surface of the rocks, were not captured by





Figs. 5 and 6.—Photographs of starfish capturing living fish.

the starfish. Such fish are very abundant about the shore, and many of them were kept in the tanks with the starfish. Such fish frequently came against the starfish, resting upon it or hiding behind it as if it were a stone. But their movements were so gentle and deliberate that the pedicellariae were not roused, and such fish were not seized.

Nature of Stimuli Causing the Food Reaction.—Why is it that the starfish sometimes feeds upon the crabs which its pedicellariae have captured, while in other cases it does not, the crabs being merely held for hours? Without question there are differences in the physiological condition of different starfish, possibly corresponding to hunger and satiety, so that the individuals vary in their behavior toward food. This matter was not studied thoroughly. But variations in behavior also depend partly of course on difference in the stimulus coming from possible food bodies. A crab certainly acts as a mechanical stimulus, and it may act also as a chemical stimulus. What are the relative effects of these two classes of stimuli in causing the starfish to feed upon a given object?

The taking of food usually begins either with the bending of the ray downward, so as to carry the food to the mouth, or with the thrusting up of the tube feet from the under side, to seize the food and carry it to the mouth. If neither of these things occurs, the body merely remains where it is held by the pedicellariae.

The effects of chemical stimulation in causing food to be taken when mechanical stimuli do not have this effect, are readily seen in the following way: A starfish holds several living crabs on its back, by means of the pedicellariae, but does not attempt to feed on them. Now one of the crabs is crushed with forceps, so that its juices diffuse into the water. At once the tube feet appear from beneath, reach upward, seize the body of the crab, pull it downward to the mouth, and feed upon it. In one case a starfish had held on its back several crabs for more than an hour. One of these was then crushed, and inside of a minute it had been carried to the ventral side by the tube feet, and was moving toward the mouth.

Chemical stimuli alone may be shown to initiate the food

reaction. If a piece of crab meat is held a little above the dorsal surface of the starfish, so that its juices diffuse against a small spot, the rosettes rise, the pedicellariae open and reach outward, as if to seize the food, and the tube feet appear from below, reach upward and feel about in a searching way. If now the bit of flesh is allowed to drop on the starfish, it is quickly seized, borne to the mouth, and eaten.

Thus chemical stimuli alone may start the food reaction. Does mechanical stimulation play any part in the matter? When a mechanical stimulus alone, such as a touch with the forceps or a quill, is applied to the dorsal surface of the starfish, usually only the pedicellariae respond, as if in defense, and there is no indication of a food reaction. But this is not always the case. Some individuals send upward their tube feet when thus stimulated; these feel about in the way characteristic of the food reaction. They may even send up the tube feet when pedicellariae are merely nipped off with the scissors. Possibly such individuals are in a state of greater hunger than usual.

Thus either mechanical or chemical stimuli alone may at times start the food reaction. Chemical stimuli are commonly more effective, and as a rule these must be added to mechanical stimulation before the food reaction occurs.

Of course intense or injurious stimuli of either class do not cause the food reaction. It is as a rule only when there is such a combination of stimuli as might well come from a body fit for food, that the starfish begins the food reaction. Of course, the fact that it may sometimes begin this reaction in response to light mechanical stimuli is quite in harmony with this statement, since such stimuli are commonly the first indications of a body fit for food.

The main features of the taking of food have now been described. There are certain points of interest that did not fall naturally into the general account; these may be spoken of here.

As we have seen, the food is often first captured by the pedicellariae, and is taken from them by the tube feet and carried to the mouth. Do the pedicellariae release the food, opening of their own motion, when it is taken by the tube feet? Observations directed upon this point seem to show clearly that they do

not. The tube feet merely pull the food away from the pedicellariae, the latter meanwhile holding on stoutly. As we have before noted, objects can usually be pulled out of the jaws before the stalk of the pedicellaria breaks, and this is what happens when the food is taken by the tube feet.

The tube feet are frequently compelled to do much feeling about before they find the object seized by the pedicellariae. No irresistible tropism bears them straight to the food. A typical example of their action in finding food is the following: A bit of crab flesh was placed on the dorsal surface of a ray near its tip: here it was seized by the pedicellariae. Now the tube feet came from beneath the ray and began to feel about in all directions. Some gradually began feeling upward, around the ray. The movement in this direction increased, the tube feet coming up especially from one side of the ray, and extending over the dorsal surface and the other side. Now the tip of the ray began to *turn* in the same direction in which the tube feet were reaching, —this movement of course neither aiding nor hindering the attainment of the food, since the food and the tube feet were moved the same distance in the same direction. At the same time the tip of the ray was raised and waved about, bending mainly to the side toward which the tube feet were reaching. Finally, among all these varied movements, some of the tube feet succeeded in reaching the bit of meat; then many more were at once applied to it, and in about four seconds it had been transferred to the ventral side of the ray and was traveling toward the mouth.

There are two main methods of conveying food to the mouth. Large objects are usually carried by the active bending of the ray beneath the body, till the object is applied to the mouth, as described above in our account of the capture of a crab. Small pieces of flesh are transported in a somewhat different manner. After being carried to the ventral side of the ray, near its tip, perhaps the ray bends downward and under at precisely the point where the food body touches it, so as to bring the food into contact with a point on the lower surface of the ray nearer the disk. The tube feet of this nearer point then seize the flesh while the more distal ones release it. Now the point at present

bearing the food bends downward, applying it to a new region, while the point first bent straightens out. Thus the food is passed from one set of tube feet to another, slowly along the under side of the ray till it reaches the mouth.

When the stomach is passed out of the mouth in feeding, it usually appears as five yellowish lobes or sacs. These fold about the prey, partly envelope it, and insert themselves into its cavities and angles. But the prey is never, so far as I have observed, actually within a sac formed by the stomach; it merely has these lobes closely applied to it. The lobes seek out especially the soft parts of the food, leaving hard parts as a rule quite uncovered. The stomach lobes are transparent and contain a clear yellowish fluid. Sometimes *Asterias* everts the stomach and applies its lobes to the surface of the glass bottom of the aquarium, apparently absorbing the mucus and other organic material which has formed a layer over the surface. In one case the lobes extended thus two or three centimeters from the mouth, reaching more than a centimeter beyond the edge of the disk, so as to be seen from above. The lobes moved about freely, exploring the surface. They were withdrawn as soon as the starfish was disturbed.

Behavior of the Starfish in Selecting the Conditions of Existence.

We have thus far seen how the starfish gets the material for carrying on its chemical processes,—food and oxygen,—and how it protects the delicate organs that are engaged in getting oxygen, by the action of the pedicellariae. But there are other requirements for existence. The starfish must live under proper external conditions if the life processes are to continue. It must not be crushed; it must not be poisoned; it must not be too hot or too cold. Many of the common agents of nature tend to injure or destroy it. How far does the starfish succeed in keeping itself under conditions that are favorable to its life processes, and how does it do this?

Undoubtedly the fact that the adult starfish is found in conditions which favor its life processes is partly due to the fact that all those which were not under such conditions have died. The

starfish produces thousands of young; these fall upon all sorts of conditions, favorable and unfavorable. Those which fall upon decidedly unfavorable conditions never become adults, so that, of course, we do not find adult starfish under such conditions. But we can place the starfish under unfavorable conditions, and through changes in the environment this often happens in nature. If now the starfish made no movements it would soon die. The movements are clearly of such a character, on the whole, as to help the starfish to avoid unfavorable conditions and to find favorable ones.

When the starfish is undisturbed in the natural conditions that are throughout favorable to its life processes,—under a stone, protected from the waves and the light, with plenty of oxygen and food,—it keeps rather quiet. Only as it begins to lack food or other necessary things does it move about.

Exploratory Movements.—But if the starfish is removed to a new situation, or if it is disturbed in almost any way,—as for example when it is removed from the large tank to a small one that serves for observation,—it soon begins to move, and usually spends a long time exploring and feeling about. Two or three rays are raised from the bottom and swing first in one direction, then in another, waving about in the water, as if searching for some object. Meanwhile with the other rays the starfish is creeping about as rapidly as it can. On the rays that are "feeling about" the tube feet are extended,—especially at the tip, but also elsewhere;—these are likewise performing "feeling" movements, waving about from side to side and exploring all the region which they can reach. A starfish placed in a jar of water on the observation table usually soon explores the entire vessel in every part, essays climbing out of it here and there, and becomes as it were acquainted with everything to be found in the region, before it settles down. Such active exploration usually lasts half to three-quarters of an hour before the animal comes to rest. And after a short period of rest the animal often begins exploring again, though usually it does not continue so long as at first.

It is evident that these exploratory movements may be of great use to the animal in a region which it has not before ex-

perienced. They subject it to all possible different conditions found in this region. If now it reacts in an adaptive way to the conditions met, remaining in or following up those conditions that assist its life processes, and withdrawing from those that do not, then its movements will be of great help to it. How far does it do this?

Adaptiveness of the Movements.—It requires, of course, only most casual observation to perceive that the starfish does do this in at least a large degree. It withdraws from all sorts of things that injure it,—injurious mechanical stimuli, heat, all sorts of harmful chemicals, fresh water, air, obstacles, etc., etc. It is evident that its movements are on the whole adaptive in a high degree; that if the starfish did not thus withdraw from injurious things it would, under the conditions arranged by the experimenter, quickly be destroyed.

While the starfish thus avoids most injurious things, it is equally clear that it follows up conditions that are beneficial to it. It follows food, either when it comes in contact with it, or is reached by chemical stimuli from it (see the numerous interesting experiments of Romanes and Preyer on this matter). I have already given, in the account of the food reactions, descriptions of the following up of food by the starfish (see pages 86 and 93). If placed between heat and a moderate temperature, between air and the water, between a crushing weight and freedom, the animal moves toward the condition that is favorable to its life processes. How living things happen to possess this extraordinary property of selecting those things which aid the life processes is perhaps the deepest question of behavior.

In the following we wish to study in some detail what conditions are rejected, what followed up, and how these movements are brought about in the starfish. Some most erroneous ideas have taken root of late in regard to this matter.

Current Erroneous Explanation of the Negative Reaction.—The fact that the starfish moves away when one of its rays is pinched or otherwise subjected to an intense stimulus has been explained very simply as follows:

"Romanes found that when one arm of a starfish is stimulated, the animal moves in a direction opposite to the stimulated

arm. This also looks like intelligence, for the animal seems to be able to avoid a danger. The late Professor Norman called my attention to the fact that when one arm of a starfish is stimulated the feet of this arm are drawn in and the arm becomes inactive. This is, however, only true of the stimulated arm; the others remain active. Therefore, according to the parallelogram of forces, a movement away from the point of stimulation takes place. Intelligence plays no part in this phenomenon." (Loeb, 1900, p. 65).

We are not here concerned with the question regarding intelligence, but only with the explanation of the movement of the starfish away from the side stimulated. It is certainly difficult to conceive how such an explanation could be given by anyone that had observed with care the locomotion of the starfish. It is possible that in some cases when one ray is stimulated locomotion takes place entirely with the other rays, but such cases are very rare; though I have watched carefully for this, I have never seen one. As a rule the walking away from the stimulated region is due, like the usual locomotion of the starfish, to the coöperation and coördination of the tube feet of all the rays. To imagine that the tube feet of each ray merely pull toward that ray, and that locomotion follows merely in the direction of the resultant of these discordant pulls, partly against the action of the tube feet of certain rays, is to have an extraordinarily crude and mistaken idea of the behavior of the starfish. The active tube feet of all the rays are pushed forward in the direction in which the starfish is going; their suckers attach themselves, and by the contraction of the tube feet (in the way described below) the starfish is carried forward, the action of all the tube feet aiding in this. Thus the tube feet of each of the five rays have a different movement from those of the other rays. In the anterior ray the feet are pushed toward the tip; in the posterior ray or rays they are pushed toward the disk; in transverse rays they are set transversely to the long axis of the rays; in oblique rays they take an oblique direction. All the tube feet are extended in such a way as to be parallel. There is a single coördinated impulse, causing all to coöperate in moving the starfish in a given direction. This coördinated extension of the tube feet

under a unified impulse is well seen in the photograph shown in fig. 13, though in this case the impulse was directed toward righting an inverted starfish, rather than toward locomotion. We shall have occasion to study thoroughly this unified impulse, later, in examining the righting reaction.

Method of Locomotion in the Starfish; Erroneous Current View.—There is a further mistaken conception expressed in the accounts commonly given of the locomotion of the starfish, and this doubtless forms the foundation on which the erroneous theory mentioned in the preceding paragraphs was based. The common mistake lies in attributing too great importance to the *pulling* of the tube feet as they shorten up after the suckers have attached themselves. The starfish is supposed to haul itself along, as one might do by attaching ropes in front, then shortening them. This is certainly a mistaken idea, so far as the usual locomotion is concerned.

My attention was directed to this fact when, holding the usual view, I endeavored to prevent the active locomotion of the starfish by placing it on loose sand or on greased surfaces. To my surprise the starfish was able to walk approximately as well under these conditions as when placed on stone or clean glass. It is obvious that when the starfish is placed on loose sand it cannot pull itself along by attaching the suckers to a firm object and then pulling upon this as a fixed point. If even the lightest pull is exercised, the sand grain to which the sucker is attached is at once lifted. And on a smooth greased surface the attachment of the suckers is prevented.

Careful study of the locomotion when on loose sand, and comparison with the usual locomotion on a solid body, showed what the real method of action is. It is the same on the sand as elsewhere,—save when the starfish is climbing a steep surface or hanging inverted from beneath a surface.

The typical method of walking is clearly as follows: Each tube foot is extended forward, in the direction in which the animal is moving (thus at different angles to the ray axis in different rays, as shown above). Then the tip of the foot is placed against the surface, the sucker aiding to give it firm attachment, and the whole tube foot is given an impulse to swing back (with

reference to the body), just as is the leg of a higher animal. That is, the tube foot acts as a lever for swinging or shoving the body forward, not as a rope for hauling it forward. Since the tip is against a solid body and does not slip, the impulse to swing back results really in moving the body forward, just as in ourselves or the horse; there is no actual swinging back of the distal end of the foot, but a swinging forward of the proximal end with the body attached to it. The tube foot acts as a partly rigid lever, though it becomes curved more or less, and may shorten or lengthen, in the act of walking. The walking of the starfish is therefore mechanically similar in essentials to that of a higher animal, the suckers merely serving for getting a firm foothold.

As the tube feet after attaching themselves swing the body forward, they do not pull; on the contrary they *push* backward a certain amount, just as do the feet of a higher animal. This becomes clearly evident when the animal is watched from the side while walking on loose sand. The sand grain to which a tube foot is attached is not lifted up as the body moves forward, though the lightest pull would suffice for this. But often it *is* pushed back a little, in the case of very loose sand, showing that the action is like that of the leg of a higher animal when a stone on which it has stepped rolls backward as the animal moves forward.

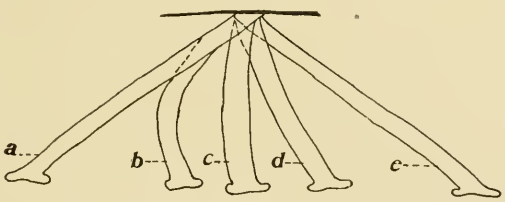


Fig. 7.—Diagram of the movement of a tube foot in locomotion. The letters *a* to *e* show successive positions of the tube foot. The forward movement of the starfish is of course not shown in the diagram.

When the tube foot is first pushed forward, it is long (fig. 7, *a*). As the body moves forward the stalk of the foot becomes shorter and somewhat curved, while the body is raised a little (fig. 7, *b*). Next the tube foot becomes longer and straightens as it becomes inclined backward; it seems to aid in pushing the body forward, for the grain of sand to which it is attached is still not

lifted, and the foot remains stiff and solid. As the body is moved still further forward, the tube foot can no longer push; it begins to shrink and shorten; and now, for the first time it lifts the sand grain to which it is attached. This sand grain is held and carried forward for a second or two; then it drops; the tube foot now extends forward again and repeats the whole process.

Walking takes place in practically the same way on a level solid body as on loose sand, so that it is doubtless brought about in accordance with the same principles. If beneath one ray of a starfish walking on sand a glass plate is laid, so that the feet of this one ray walk on the solid, their action is indistinguishable from that of those walking on the sand. There can be no doubt therefore but that the common notion that the starfish in its locomotion *pulls* itself forward is a mistaken one. The suckers serve a useful purpose in preventing the feet from slipping. As is, of course, well known, there are many starfish that have no suckers on their tube feet; they walk in essentially the same manner as is described above.

In a starfish having suckers, it is a notable and significant fact that during locomotion the animal is not firmly attached to the substratum. Often a quiet starfish is so attached by its suckers that it can scarcely be freed by force from the object on which it is resting. But if we can in any way get it to begin walking, we can by quick action pick it up with the greatest ease. This in itself seems to show that the attachment of the suckers is not a particularly important point in locomotion.

It is one of the most remarkable characteristics of animals that they are able to accomplish the same ends in various ways. I would not, of course, for a moment maintain that the suckers are not essential when the starfish walks up the perpendicular side of an aquarium or a stone, or when it hangs from the under side of a surface. But even in these situations, while the suckers are necessary for attachment, the actual locomotion seems to occur rather by the action of the tube feet as levers, in the way described above, than as cords for pulling the animal along.

It is evident that to understand how the animal responds to stimuli, it is necessary to have a clear idea of the nature of its usual movements, otherwise one is likely to be led into bizarre

errors. This remark applies as well to the study of the behavior of other animals as of the starfish.

Three Classes of Protective Reactions.—Turning now to the movements of the starfish under the action of different agents, we find that it has not merely one, but at least three different protective reactions when a certain point on its body is injured. If for example we pinch the tip of a ray of the starfish, the animal may, instead of fleeing, shrink down close against the surface on which it is lying, and attach itself firmly with its tube feet. It can then be removed only with great difficulty. This is perhaps the commonest reaction of the starfish to any sudden attack, and it is certainly very effective in preventing the attacker from dislodging or carrying the creature away, as I can testify from my own experience.

The second reaction to an injurious stimulus, usually combined with the one just mentioned, is the rising of the rosettes, the opening of the pedicellariae, and their seizure of any object which they can reach. This has been considered.

The third possible reaction is that of movement away from the side stimulated, in the way described above.

A given stimulus may cause in one specimen one of these reactions, in another another, or if a given stimulus is repeated, it may first cause one of these reactions and later another. Thus, two starfish were lying side by side. The middle of a ray was pressed with a glass rod, as nearly as possible in the same way on each. One responded by a rising of the rosettes in the ray pressed, and by taking hold firmly of the substratum with all its tube feet. In the second specimen neither of these reactions was given, but the animal began instead to move slowly away. If the pressure was made a little greater, this animal stopped, took hold firmly with its suckers, and attacked with its pedicellariae. Two minutes later an equally strong pressure on the same spot caused only a rapid movement away, without attack on the part of the pedicellariae. These examples are typical of the variations to be observed.

Reaction to Light.

The reaction by movement in a certain direction may be induced, as we have seen, by mechanical, thermal and chemical stimuli of many kinds,—these including most of the agents which act on the starfish under natural conditions. The locomotor reaction may also be induced by light. We must describe the main features of the reaction to light, since an understanding of this reaction is necessary for comprehending many important points in the animal's behavior. An exhaustive investigation of the reactions of this animal to light would be of great value; such an investigation I was unable to make in the time at my disposal. But the main outlines of the behavior may be given.

It should first be noted that while the reaction of this starfish to light is very striking, it is likewise extremely variable, and is often modified or quite prevented by various internal conditions, as well as by external influences. I give first the characteristic reactions to light when no interfering influences are at work.

Unlike most starfish whose reactions to light have been described, this species is decidedly negative to light of ordinary intensity. This is shown in the following different ways:

(1) When the vessel containing the animal is placed near a window or other source of light, the starfish crawls directly away from the lighted side.

(2) When transferred without other disturbance from a dark region to a light one, the starfish becomes much disturbed and begins to creep about actively.

(3) If part of the body of the starfish is shaded, the animal moves toward the shaded side, and after exploring a vessel in which it is confined, it takes up a position in the region sheltered from the light, and there comes to rest.

(4) If confined in a field uniformly lighted from one side, so that the animal is unable to get out of the light, it takes a peculiar position, such that what are apparently the more sensitive parts of the body are sheltered from the light.

(5) When turned on its back, it tends, in righting itself, to turn toward the side away from the light.

We will take up in order certain facts concerning each of these methods of action.

Movement away from the Light.—For many purposes the starfish was observed in round glass vessels placed on a table near a window. Under these conditions it is observed that the starfish, when not distracted by other sources of stimuli, moves directly away from the window, to the opposite side of the vessel. It may thus move with any ray or any interradius in advance.

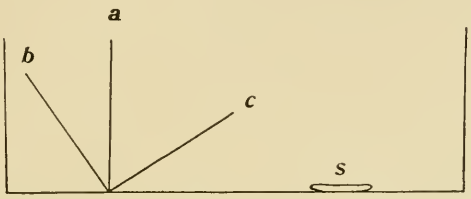


Fig. 8.—Diagram of the different positions of the screen in the experiments described in the text. The light is supposed to come from the right. The starfish is at *s*.

It was suggested to me by one of the investigators in the laboratory that the light was reflected in a concentrated condition from the concave inner surface of the side of the vessel away from the window, and that this reflection formed the main source of light for the starfish. The animal would then be moving toward the strongest light, and would be really reacting positively instead of negatively. This was tested in several ways. (1) The inner surface of the vessel was covered with black cloth, save on the side next to the window, so that there would be little reflection. The starfish moved away from the window as before. (2) A black screen was placed behind the starfish,—on the side away from the light. This screen was placed sometimes perpendicularly, sometimes inclined toward the starfish, sometimes inclined away from it (fig. 8). When the screen is inclined away from the starfish (*b*) such reflected rays as exist are, of course, directed upward into the air, and not toward the starfish at all. When the screen is inclined toward the starfish (*c*), a dark pocket is formed in the back of the vessel, into which the starfish is moving. In all these cases it moves as readily as before, away from the window or other source of light. There can then be no doubt but that the reaction is really a negative one; this species of *Asterias* tends to move away from the side from which the light comes.

When the light coming from one side is very weak, there is no reaction. Precise quantitative experiments were not made. But when the starfish was placed in a vessel in a dark room, lighted only by a small hole on one side, they moved without reference to the light. In no case was there evidence of a positive reaction to light.

2. *General Stimulating Effect of Increased Light.*—When a starfish that has been in comparative obscurity is subjected to strong light, the animal becomes much roused up and begins to move about and explore actively. If possible it usually goes first away from the source of light; if this is not possible, it follows the walls of the vessel, creeps around it, climbs up to the surface, waves its rays and tube feet in all directions, essays climbing out of the vessel (in the way described later), and in general conducts itself in a most perturbed manner. If at the moment when the light is increased it is engaged in any special activity, it usually ceases this to begin its apparent attempts to escape. If it is eating, or is holding prey with its tube feet, it ceases eating or releases its prey. This proved especially troublesome when we were attempting to photograph the starfish while eating or capturing food (figs. 2, 5, 6). As soon as increased light was thrown on the animal in order to give opportunity for a photograph, the prey was released[4]. But after twenty minutes to three-quarters of a hour, the starfish becomes accustomed to a moderate light, such as that coming from a cloudless sky. It may then settle down quietly again and resume its interrupted activities, recapturing its prey and continuing its meal.

3. *Movement toward Darker Regions, and Coming to Rest in the Shade.*—After exploring the vessel in which it is confined, the starfish usually comes to rest in that part of the vessel that is best protected from the light. In a cylindrical jar it finally stops as a rule on the right or left side, where the curving of the jar serves to refract and reflect the light so as to leave a region less illuminated than elsewhere; here the starfish presses itself close against the side and comes to rest. Loeb (1893) has observed that negative flatworms often take a similar position. If the vessel where the starfish is confined contains opaque bodies, the starfish commonly places itself behind one of these.

[4] The holding by the pedicellariae is not thus affected by the light.

Thus the starfish tends to come to rest in darkened regions. It likewise tends to move from a lighter to a darker region. If, in a region lighted mainly from above, one-half or one-third the starfish is shaded by a screen, the animal as a rule moves toward the shaded side, and gets behind the screen.

4. *Direction of Light Rays versus Differences in Illumination.* —We find then that light determines locomotion in two ways. (1) The starfish tends to move away from the source of light (thus in the direction of the light rays). (2) It tends to move from a lighter to a darker region.

What will happen when the two directions of movement thus defined do not coincide? If the dark region lies to one side, or nearer the source of light, will the starfish move into it, or will it move away from the source of light, even though this takes it into lighter regions?

This is essentially the problem which has been so much discussed for many organisms, and which is commonly put as follows: What is the relative efficiency of the *direction of the rays of light*, as compared with *differences in intensity of illumination* on different parts of the body, in determining the direction of movement? An animal so large and so peculiarly formed as the starfish offers exceptional advantages for the study of this problem, and it should be attacked here with such precise means as have recently enabled Mast (1906, 1907) to settle the question for certain lower forms.

But it may be pointed out that the form in which this general question is stated above is perhaps a misleading one. When the starfish is placed in a field lighted from one side, the body of the animal of course itself casts a shadow; that side or surface of the body away from the light is not illuminated. Thus there are in all cases differences in the intensity of illumination of different parts of the body. Further, when the starfish moves in the direction of the rays of light, away from the source, it is of course moving *toward the unilluminated side* of its own body. It appears to be impossible to so arrange conditions that the effect of the direction of the rays can be tested independently of differences of illumination.

Thus the problem is perhaps merely this: When there are

inequalities in illumination due to different objects, will the starfish move toward the shade cast by its own body, or toward that due to some other object[5]?

Experiments answer this question in exactly the way that might be anticipated, when it is put in this form. The starfish sometimes moves toward the shadow cast by its own body (*i. e.*, in the direction of the rays of light), sometimes toward the shadow cast by some other body (*i. e.*, toward the less illuminated part of the field). Which of the two factors shall prevail when both are present appears to depend, other things being equal, on the relative extent of the two shaded regions. It is not possible to compare precisely the extent of shade cast by the body of the starfish with that due to some other object, so that the relation cannot be expressed in an accurate quantitative way. Moreover, the shade cast by the starfish itself commonly affects mainly the ventral surface of the animal, while that due to other objects affects mainly the dorsal surface, so that the effects of the two may not be strictly comparable. But the following experimental results show that the general relation is as stated above.

(1) If the starfish is placed in a flat vessel with the sun shining on it from one side, and no part of its body is screened from the sun, it of course moves directly away from the sun (*i. e.*, toward the shadow cast by its body). But if that half of its body next to the sun is shaded by a black screen, so that only the distal half is in the light, then the starfish moves as a rule into the shadow cast by the screen, and thus toward the sun and against the sun's rays. If less than one-half the body was shaded in this way, the results were variable. Sometimes the starfish moved into the shade of the screen (and toward the sun) when only a part of certain rays was shaded; at other times it moved under such conditions away from the source of light. If the experiments are carried on in a flat vessel with opaque sides, the sunlight coming slantwise from above, the starfish if partly shaded by the side of the vessel next the sun often moves toward that side, hiding itself in the shadow.

[5] It would appear that the problem might be similarly put for any other organism.

Similar behavior is seen when a screen is so placed that its shadow falls across the middle of the body, parallel with the rays of light, so that one-half of the body is shaded, the other in the light. The starfish moves toward that half of the body that is shaded by the screen,—therefore nearly at right angles to the direction of the sun's rays. But the movement is slightly oblique, the path being directed a little toward the side away from the sun. In other words the starfish moves both toward the shadow cast by the screen, and that cast by its own body, the former preponderating in influence. With the same starfish the screen may be transferred repeatedly from right to left side and back; in each case, after some delay, the starfish changes its direction of movement and creeps into the shade.

If the screen is so placed as to cover in successive cases less and less of the body, its influence on the movement becomes less; the path of the starfish forms a smaller and smaller angle with the direction of the rays of light. If less than one-half of the length of the rays of one side is shaded there seems to be little or no effect on the movement; the starfish creeps directly away from the source of light.

These results show clearly that the relative intensity of illumination on different parts of the body of the starfish may, and does at times, determine the direction of the movement, without regard to the direction of the rays of light. Furthermore, *all* the experimental results are explicable on this basis, since in a field uniformly lighted from one side the body of the starfish itself serves as a screen to keep a part of its surface unilluminated; the animal then moving toward this unilluminated half. The results agree with those of the very careful work of Mast on lower organisms. The thorough work of recent years seems to strengthen the contention of Holt and Lee (1901), that there is little if any positive evidence of the "efficacy of pure direction" of rays of light in determining the movements of organisms. In all cases the results can be equally well understood on the view that the organism tends to move toward the most (or least, as the case may be) illuminated region; and many of the facts admit of no other explanation.

5. *Position Taken when the Starfish is Confined in a Uniformly Illuminated Field.*—When the starfish is placed in a shallow vessel with strong light coming from one side, so that

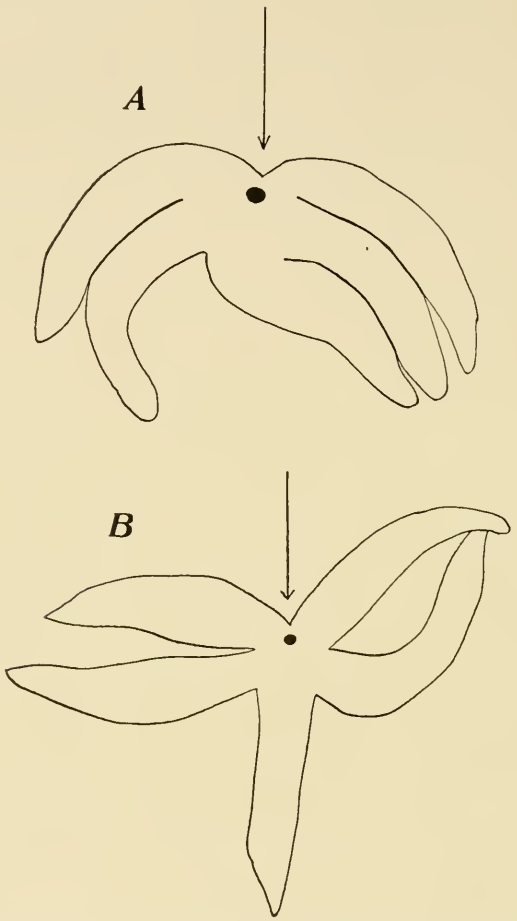


Fig. 9.—Outlines of the position of orientation in two resting starfish. The direction from which the light comes is indicated by the arrows.

there is no chance to find a dark region, the animal takes a characteristic position. If it is resting on a uniform flat surface, it directs the tips of all the rays away from the lighted side, so that it becomes characteristically of a bilaterally symmetrical form (fig. 9), though of course with some divergences from this form.

The two rays on that side of the body next to the light are curved to right and left, as shown in the figures, so as to leave a wide gap between them; while the distal ray either extends straight out (fig. 9*B*) or is brought near or against one of the other rays (fig. 9*A*). An important feature of the orientation, that cannot be brought out in the outline figures, is the following: the rays are so twisted that the ventral surface is very completely protected from the light. The two rays on the lighted side are slightly inclined on their long axes so as to make the dorsal surface face the light, while the ventral surface is completely covered. The other rays are either similarly tilted, or are so placed that their lower surfaces are well sheltered by the rays next the light (fig. 9*A*). The entire position looks like an attempt on the part of the animal to protect the ventral surface and the tips of the rays from the light. That this is indeed the case is indicated by the following facts: (1) If when the starfish is oriented as shown in fig 9, light is reflected from beneath, either from a mirror or a sheet of white paper, so as to strike the ventral surface, the starfish soon moves away. (2) If while in the position of orientation the starfish is turned so that the light strikes the tips of the rays and the partly exposed ventral surface (though the animal is still symmetrical to the rays) it after a time moves away from the lighted side, and in time reverses its position, again inclining ventral surface and tips of the rays away from the light. (3) Commonly, when exposed to the light from one side, the starfish creeps to that side of the vessel farthest away from the light, then places itself in the angle between that side and the bottom of the vessel, with the ventral surface completely hidden from the light, while the dorsal surface is fully exposed. If now we turn the vessel around, so that the light shines on the ventral surface, the starfish is roused and begins to move about until it again gets into a position with the ventral surface directed away from the light.

It is worth while to notice that in this position of orientation the starfish receives the same amount of light as when it is turned around with ventral surface to the light. The efforts of the animal seem directed toward protecting the ventral surface, and, to a less degree, the tips of the rays. The ventral surface is of

course little pigmented, and is probably more injured by strong light than is the dorsal surface.

But when it is possible for the starfish to move so as to decrease the illumination of the body as a whole, then, as we have before seen, it does so, creeping into a shadow.

The protection of the tips of the rays from the light seems much less striven for than the protection of the ventral surface. In some cases the starfish comes to rest in the light with ventral surface well protected, but with the tips of the rays so elevated and curved that the eye spots are in the light. After it has been at rest for a time, however, the eye spots are usually so placed as to be protected from the light.

When the starfish is exposed to a strong light from one side, it commonly moves before coming to rest, as we have seen, away from the source of light. While thus moving, the position of the rays varies much. Often there is no indication of the curving of the rays so as to take the bisymmetrical form shown in fig. 9. In other cases such a shape is gradually assumed while the movement is in progress. In all cases, so far as observed, the rays are inclined while the movement is taking place, in such a way as to direct the ventral surfaces away from the light. It may be asked whether this is not a mere incidental result of movement, the ventral surface being always directed toward the side toward which the animal is moving? Observation shows this not to be the case; at least if there is any such turning of the ventral surface in a starfish moving when not illuminated from one side, it is hardly noticeable, and is not to be compared to the pronounced turning away from the light when the starfish is illuminated from one side.

6. *Effect of Light on the Righting Reaction.*—This will be discussed in our account of the righting reaction (p. 135).

7. *Vision in the Starfish?*—Throughout the reactions to light as thus far described, the effects have apparently been due entirely to the relative illumination of different parts of the body. The starfish moves in each case toward that part of the body that is least illuminated.

The question may arise as to whether there exists in the starfish anything resembling what we speak of as image formation,

resulting in the perception of objects, or at least in a reaction toward objects as such. The recent interesting work of Cole (1907) shows that something of this sort is found in many lower animals. Certain of my observations on the starfish seemed to indicate that something of the sort may exist in this animal. But the results of observations on this matter were so inconstant and varied so much with different individuals, that their significance is uncertain. I give some of the facts merely as suggesting further work along this line.

It was noticed that if the starfish were exposed to the light in a flat vessel with low, opaque sides (galvanized iron or the like), they often did not behave in the same way as when similarly exposed in a vessel with glass sides. In the latter case they commonly move straight away from the source of light. In the vessel with opaque sides, they frequently move instead toward that side of the vessel that is nearest to them. This is not a matter of light and shade, for it occurs *when the side toward which the starfish moves is in the full light, and casts no shadow in the direction of the animal.* These relations are illustrated in the following experiment:

Side by side were placed a galvanized iron pan 40 cm. long, with sides 6 cm. high, and a large glass vessel of nearly the same size. The vessels were placed in the direct sunlight, and in such a way that the sides of the opaque vessel did not cast shadows into the pan save on the proximal end,—the right and left sides being parallel with the sun's rays. Now I placed one after another seven starfish in the iron pan, and observed their movements. They were placed in various parts of the pan, but always in such a way that the shadow of the side next the sun did not fall upon any part of the animals. Only one of these starfish moved directly away from the source of light, in the direction of the sun's rays. Three that were near the left side of the pan moved directly toward that side. Three others, that were near that side of the pan next the sun (though not at all in the shadow of that side), moved directly toward that side (hence toward the source of light), and placed themselves in the shade. Now these same seven starfish were transferred one after another to the vessel with glass sides, some nearer one side, some another.

All went directly away from the lighted side, in the direction of the light rays. Replacing them in the iron vessel, each went as before (with one exception) toward that side of the vessel that was nearest it. It appears most decidedly as if the animals were able to perceive the dark sides from a short distance, and to move toward them, even though these sides cast no shadow.

Now the following experiment was tried. The starfish was placed in the center of a large flat surface, in the sunlight, far from any object. Then a black plate 12 cm. wide and 16 cm. long was placed at one side of the animal, in such a way that its shadow did not fall on the animal, the plate being about 2 cm. from the tips of the nearest rays. Thereupon these nearest rays were raised and began feeling about, and soon the starfish began to move toward the black plate. The plate and starfish were now removed, then replaced on the flat surface as before, save that the plate now stood in a different direction from the starfish. The animal moved toward it, as before. This was done a third time, with the same results. In another case a starfish was induced to move repeatedly toward a black ruler that was placed upright about two cm. from the tip of a ray.

It will naturally suggest itself to the reader that the proper method of experimentation is as follows: The plate is placed to the right of the starfish. As soon as the animal begins to move toward it, the plate is transferred to the opposite side, in order to determine whether the starfish will reverse its movement and follow the plate. While this experiment succeeds in a few cases, it is as a rule doomed to failure from beforehand, owing to a marked characteristic of starfish behavior. When the animal gets started in a certain direction, it tends to persist in that direction without regard to changed conditions,—a matter which we shall discuss later (p. 115). Thus, if the plate is transferred to a new position, the starfish continues to go in the direction in which it has started, until it has gone too far to be affected by the plate.

It may be suggested that the movement toward the plate was due merely to the disturbance in the water induced by the introduction of the plate. There is no doubt but that the starfish does sometimes move toward the seat of such a disturbance. But when the plate was introduced first and the starfish after, the

results were the same. Moreover, the movement toward the opaque sides of the containing vessel could not be explained in this way.

But one fact needs emphasis. The number of individuals experimented on in this way was small (only about a dozen), and fully half of these *moved without any reference to the position of the plate or screen.* Yet those that did respond, reacted so constantly and clearly that the results can hardly have been accidental. Statistical work with a large number of individuals will be required to set this matter in a perfectly clear light. The work with light was subsidiary to the main objects which I had in view, and therefore this matter could not be investigated thoroughly in the time at my disposal. But I believe that all the facts herein set forth are new in the behavior of starfish toward light.

Positive Reactions.

Not only does the starfish retreat from those things that tend to interfere with its physiological processes, but it follows up those which assist these processes. It follows food, either on coming in contact with it, or when it is reached by characteristic chemical stimuli from the food; this has already been discussed (pp. 84-94). The reaction is, as we have seen, not a stereotyped, irresistible tropism; the animal frequently feels about a great deal before it finds the food. A typical example of this is given in our account of the food reactions (p. 93).

Positive reactions take place toward indifferent objects, such as stones, depressions, roughenings of the surface, etc., when the circumstances are such that movement toward these objects is likely to be advantageous. These are reactions to what I have elsewhere (1906) called representative stimuli,—the present stimulus not being beneficial in itself, but leading to or representing the beneficial results that follow upon a positive reaction toward it. Examples of such reactions are given in a later section (p. 114).

In the positive reactions, as in the negative ones, the starfish usually moves with a unified impulse,—all the tube feet of all the rays being directed toward the object toward which the starfish is moving.

Factors Determining the Nature and Variations of the Reactions to Given External Stimuli.

We have now seen the typical negative and positive reactions to certain classes of stimuli. But the reactions to a given stimulus or class of stimuli are by no means invariable; on the contrary they vary much, depending on many factors, internal and external. It is not possible to classify these different factors in any precise way, since they interact in a complicated manner, so that the effect of each varies in different cases. But we shall attempt to deal with some of the more important of these factors, under the following heads:

1. *Interaction and Interference of Stimuli.*—As we have seen, the starfish when illuminated from one side usually moves away from the source of light. But if under these conditions the tips of the tube feet of a ray come in contact with some object, as a pebble or the side of the vessel in which the starfish is situated, the animal at once begins to move toward this object. It may then move at any angle with the light, or even directly toward the source of light. The starfish may usually be induced to move directly toward the sun by placing it in such a position that the tip of a ray comes in contact with the side of the glass vessel (or with any other object) on the side directed toward the sun.

This reaction is closely related to that described previously, in which the starfish when subjected to strong light moves toward an object near by, even though it may not be in contact with that object nor shaded by it (pp. 110-113). By thus moving toward any object, the starfish is of course likely to find protection from the light more readily than by simply fleeing straight away from the sun, so that the reaction has an evident regulatory value.

When the animal reaches the object toward which it has moved, it usually explores its surface, or if it is large, follows along it, until it comes to a region where it is protected from the light. If it thus comes in contact with the sides of a glass vessel, it may thus follow the wall completely around the vessel, moving part of the time away from the light, part of the time obliquely, part of the time transversely, and part of the time directly to-

ward the light. Thus the usual reaction to light is completely prevented or changed when the starfish comes into relation with some object.

Any marked inequality of the surface acts in the same way as a solid object. If the tube feet find in their exploratory movements a depression, the starfish moves toward this exactly as toward a projecting object; the animal tries to force itself into the depression, seeming to endeavor to protect itself from the light.

As a result of these relations, when the starfish is subjected to light while clinging to a rock or in a tide pool, its movements are only indirectly determined by the direction of the rays of light. If there are roughenings or depressions of the rocky surface, the animal moves with reference to these, as well as with relation to areas of light and shade; it does not stop moving till it has reached a place where it is no longer subjected to strong light.

2. *Effects of Position of the Body.*—The movements under stimulation are partly determined by the position of the animal at the time stimulation occurs. Thus, a specimen had taken an elongated form, with three rays projecting in one direction, two in the opposite, with a sort of narrow waist between them (as in fig. 4). Now sunlight was allowed to fall on the animal transversely to its (temporary) long axis. This roused the starfish to activity, but the animal crept toward the middle one of the three rays (*c*),—so transversely to the light. Gradually the rays spread out; the creature took the star form, and slowly veered off, so as to finally move directly away from the source of light. Examples of such dependence of the direction of movement on the temporary form of the body could easily be multiplied.

3. *Persistence of Impulse to Move in a Certain Direction.*—We have already noticed the fact that when the starfish moves in a certain direction, it does so under the effect of a unified impulse[6], which is seen in the coördinated position and movement of all the tube feet, as well as in other ways (see pp. 97, 113). Such an impulse, when once in operation, lasts for some time, in

[6] I use the word impulse for lack of some better term, in a descriptive sense, without intending to imply anything subjective behind the action; concerning such we know nothing.

spite of changed conditions. For example, in a certain case the sun was allowed to shine on the starfish in such a way that the ray *d* was on the side opposite the source of light. The animal then began to move, as we should expect, toward its ray *d*, away from the source of light. Now the creature was suddenly seized with the hand, taken from the bottom, turned around, and replaced on the bottom in such a position that the ray *d* was directed *toward* the sun. The interrupted movement toward the ray *d* was at once resumed, so that the starfish was now moving toward the sun. If the moving animal was suddenly placed with the advancing ray transverse or oblique to the direction of the sunlight, it continued as before to move toward *d*, without relation to the direction of the light.

This persistence in a direction of movement (relatively to its own structure) when once begun, usually lasts under such conditions as we have just described only for about five to seven seconds. Then the animal is likely to stop, and slowly to begin moving away from the source of light. But sometimes it persists in a given direction much longer, in spite of change in the outward conditions. This is particularly likely to occur when the animal has been moving for some time in a given direction.

This persistence in a given direction is shown in exactly the same way whether the original source of the impulse to move is light or something else. At times a starfish shows an obstinate tendency to move toward a certain one of its rays, without much relation to external conditions. Thus, a starfish placed in a flat vessel near a window started to move toward its ray *d*,— which led it, contrary to the usual rule, toward the window. I now covered the side next the window with a black cloth, so that the starfish was going straight into the dark instead of toward the light; it continued in the same direction, the ray *d* in advance. I now took up the creature and turned it quickly around, so that the ray *d* was headed away from the dark; the starfish continued toward *d*, as before. Shading various parts of the body or rays had no effect on the movement; the animal persisted in moving toward the ray *d*, quite independently of the distribution of light and shade.

4. *Effect of Previous Stimuli.*—This persistence of an impulse to move in a certain way is sometimes evident even when the animal has not yet begun to move; it produces a striking after effect of stimulation. Thus, the starfish was placed on a smooth, flat surface. The rays began their usual exploring movements; under these conditions if one of the rays touches some object, the animal begins to move in that direction. Before locomotion began the tube feet of the tip of the ray *c* were allowed to come in contact with the side of the vessel. Now, before the starfish began to move toward that side, it was taken up and turned around, so that the ray *c* was directed toward the open part of the vessel, instead of toward the side. Now the tube feet of the ray *c* began to extend and explore, as if searching for the object which they had before touched. At the same time the feet of the other rays were moved about and extended in the same direction as were those of *c*, while the starfish began to move toward *c*. This experiment was repeated many times, and under various conditions, with the same results. Thus, when the starfish is moving on a plane surface away from a window, a solid object is allowed to touch for an instant the tube feet of one of the lateral rays, and is then removed. Thereupon the tube feet of that side extend, and the starfish sidles off in the direction in which it had touched the solid object.

The behavior of the starfish is in these relations objectively like that of a higher animal which, having experienced a certain stimulus, *searches* for this after it has disappeared. Such an animal is commonly said to show memory of the past stimulation.

These results recall and perhaps partly explain certain experiments of Preyer (1886), in which the starfish was found to have a decided tendency to move toward certain rays. Preyer gave no explanation of these results. They are discussed further in a later section (p. 150).

The strong tendency which the starfish shows to continue a movement once begun is evidently akin to the formation of a habit. One is led to inquire whether this tendency could not be increased and made lasting by repetition of a given movement; in other words, whether the starfish may not form real habits. This question will be dealt with in a section devoted especially to this matter (pp. 148-169).

5. *Effects of Physiological Condition; Reaction to the Situation as a Whole.*—As a result of the factors set forth in paragraphs 1-4, as well as of others of similar character, the behavior of the starfish when subjected to a given stimulus is extremely variable. It depends on the simultaneous presence of other stimuli, on past stimuli that have acted on the animal, on its past reactions, on the way it is behaving at the time the stimulus acts upon it, and on various other factors. These can nearly all be summed up in the statement that the behavior of the starfish under given external conditions depends on its physiological state, and that its physiological states are varied and depend on many factors.

To put the matter in another way, how the starfish shall react under given stimulation depends on circumstances, and on its past experiences. Thus the starfish while walking in a certain direction, like other animals, frequently avoids obstacles against which it comes; it reacts, as we say, negatively to mechanical stimuli. But when it has been placed in new surroundings, as in a jar or aquarium, and is moving about on a tour of exploration, it reacts for a time in the opposite manner. When a ray comes in contact with an object, the starfish turns and creeps toward that, until it has explored it well. Then, if the object presents no opportunities for a protective retreat, the starfish leaves it and moves on.

One of the things which the starfish avoids most consistently, under ordinary conditions, is leaving the water. When it comes to the edge of a pool or aquarium where the tip of a ray projects out of the water, the animal withdraws. There is of course, from the standpoint of regulation, good reason for this, since drying up is destructive. Furthermore, as we have seen, the starfish usually shows a decided avoidance of light, retreating from the lighted side of a vessel. But under certain conditions both its repugnance to exposure to air and to light are overcome for a time. This occurs when the starfish has been transferred to a new region, and is exploring it. It proceeds to explore light as well as dark regions, and even ventures to reach far out into the air. Description of a typical example will bring out the essential points in such behavior.

A large circular glass jar contained a strong, active starfish, which was now resting quietly on the bottom. Another starfish which was at rest in a large tank was transferred to the jar, which stood on the observation table, before a window. This new starfish at once began to explore its new quarters. It crept about, "feeling" with its tube feet and rays, and testing every inch of its surroundings. Among other activities, it followed around the walls of the jar, creeping part of the time toward the light, part of the time away from it. At first it abstained from thrusting its rays out of the water. But after crawling around the dish a few times, it reached again the side nearest the window, and now made a thorough exploration of the region outside the water. It climbed up the side of the jar to the edge, so that three rays and the disk were out of the water, while half of the other two rays were still immersed. It then reached out over the edge of the jar into space, at least half its diameter being beyond the edge; the three extended rays waved in all directions in the air, while their tube feet were extended and likewise made exploratory movements. This was continued seven minutes; then the starfish gave it up; the rays were withdrawn into the water, and the animal continued exploring the interior of the jar. Having crept completely around the jar, it came back to the side next to the strongly lighted window; here it began to explore again the region outside the water, climbing partly out of the jar, as before. But this time it did not reach so far outward, and did not continue the process so long as before, climbing back after two or three minutes and resuming its peregrinations. After again completing the circuit of the vessel, it again reached the side next the window, again thrust certain rays out of the water and felt about for a little, but quickly ceased and went back into the water. It explored the vessel for a few minutes more, then finally came to rest in the angle between the side and the bottom. Its exploration had lasted three-quarters of an hour. Though now no longer creeping about, it was clear that the animal was not at rest, for the tube feet still kept actively moving in one direction after another, for a time. They sometimes stopped for a few minutes, then resumed their activity. It was more than an hour after the starfish had been introduced into the jar before it

came to rest. Meanwhile, the other starfish, which had been for a long time in the jar, had seemingly become quite reconciled to it; it did not move about save when roused by special stimulation.

The behavior described above is typical; I have observed it in many cases. It takes place in the same way whether the jar to which the starfish is removed has fresh sea water running through it or not. The varied changes in behavior are clearly not due to corresponding changes in the external conditions. They are of course determined in some way, as are the varied activities of man and other organisms. Changes in the internal condition of the organism set in operation changes in the external activity.

It is clear then that the starfish does not always react in the same way to the same external stimulus. It reacts, as does a higher animal, not exclusively to one particular present agent, but to the situation as a whole, including past external factors as well as present ones. These past factors of course produce their effect through the modifications they have induced within the organism.

The Righting Reaction.

The foregoing pages have dealt with the behavior of the starfish in regulating the income of material for carrying on its life processes (food and oxygen), and in finding the proper environmental conditions,—avoiding those that are injurious and seeking out those that are favorable. We now take up a matter that is of equal importance with these, though serving to regulate the life processes in a somewhat more indirect way. The starfish is so formed that its life activities can be well carried on only when it is resting on its ventral surface. When turned over, on its dorsal surface, locomotion is impossible, the finding and capture of food must stop, the delicate gills are pressed against the bottom, injuring them and impeding respiration, and displacements of the internal organs must occur, that may be harmful to their proper functioning. We find, as might be anticipated, that there is a regulation of these bad effects by movement; the starfish turns itself again on its ventral surface. The process of turning is known as the *righting reaction*.

The righting reaction has been much studied, by Romanes (1885), Preyer (1886), von Uexküll (1900), Loeb (1900) and others, but a really thorough analysis of the factors on which it depends and of the way in which it occurs has never been made. The work of Romanes, Loeb and von Uexküll was done mainly with a view to the analysis of the functions of the nervous system. That of Preyer was done from a broader standpoint, and brings out much that is of great interest, though he did not make a careful analysis. Driesch (1903), with his usual acuteness in detecting essentials, has discussed some of the fundamental problems which underlie behavior of this character, and has noted the need of a thorough study of this and similar reactions (l. c. p. 17, 36). Driesch's discussion will be spoken of further. The purpose of the following is to give a thorough experimental analysis of the righting reaction.

A good picture of the general course of the righting reaction is given by Loeb. "If a starfish be laid on its back, the tube feet of all the arms are stretched out at once and are moved hither and thither as if feeling for something, and soon the tips of one or more arms turn over and touch the underlying surface with their ventral side. The tube feet of these arms attach themselves to this surface and the animal is then able to turn a somersault and regain its normal position. For this result it is essential that all five arms do not attempt simultaneously to bring the animal into the ventral position. Should the tips of all five, or even four tug simultaneously, it would be impossible for the animal to turn over. In normal starfish having five arms, not more than three begin the act of turning; the other two remain quiet." (Loeb 1900, pp. 61-62.)

Is this reaction stereotyped, always occurring in the same way? On this question we have Preyer's statement of the results of his extensive experiments: "Neither in one species or the other is the method of turning always the same. I have likewise seen *Asterias glacialis*, which was several times in succession turned on its back without change in the outer conditions, right itself sometimes in one manner, sometimes in another. The spirals of the twisted arms do not work each time in corresponding directions, but at first the neighboring arms often oppose

each other. But soon the correction takes place, in that the attached feet stop those that are disturbing the turning, and the wrongly twisted radii straighten out again. . . . . The variability of form in starfish that are righting themselves is great, and no species rights itself in only one way. . . . . But here, too, it is true that no *Astropecten* rights itself twice in succession in exactly the same way. An adaptation to the surface of attachment always occurs, and according as this is convex, concave, smooth, rough or inclined, is the turning process made easier or more difficult, and brought about in this manner or that." (Preyer, 1886, pp. 107-108).

Thus, according to these accounts, we have in this reaction complicated behavior, with the different organs acting in a coordinated way, some being active, while others refrain from activity,—and the whole not stereotyped, but extremely variable, —reaching the end of righting the animal in varied ways. Driesch (1903) has well emphasized the interesting character of this reaction and the importance of considering it carefully in forming our views of behavior in general. It will be well to give a brief outline of Driesch's views. He points out that such behavior is not made intelligible by the simple factors that have in many cases been set forth for explaining the behavior of the lower organisms. Particular significance is seen in the facts that (1) different parts of the body play different coördinated roles in bringing about the righting, some being active, while others refrain from activity, and (2) that the roles of the different parts are variable, but so accommodated to each other as to accomplish a unified result. On the basis mainly of these facts Driesch founds for such behavior the concept of "free-combination," contrasting it with the stereotyped course of reflexes and instincts. Such "freely-combined" behavior Driesch considers as at least a transitional stage toward that seen in the complicated "actions" or "conduct" ("Handlungen") of higher animals and men. Furthermore, for such "Handlungen" Driesch believes that an analysis into factors of the same sort as we find in inorganic processes is impossible. He holds that an unanalyzable entity which he calls a "psychoid" or "entelechy" in some way controls the behavior in the interests of the organism

as a whole. Whether he would explicitly postulate such an entity for the particular case of the starfish I will not endeavor to assert, but this would seem to be the logical result from his general discussion.

It is clear that such behavior presents problems of great interest, and for their discussion we need above all things a thorough knowledge of the facts. Preyer's account has been questioned; how far is it correct, especially in the matter of the variability of the reaction? Does an extended study of the facts justify the deep significance that Driesch has given to this behavior? And how far does his general theory assist us in understanding it?

These and other questions will be kept under consideration in the following account. Our method shall be to give an empirical analysis, (1) of the various factors which determine the behavior; (2) of the various factors which compose the behavior, followed by (3) a discussion of the results. The account is based on a very large number of experiments and observations. I have in my notes written records of the way the reaction occurred in 1220 cases, and a very large number of observations were unrecorded. It is hoped therefore to make the analysis fairly adequate.

Before beginning our account, it will be well to give outlines of the starfish, with the designation of the five rays that we shall employ throughout our account, as well as to define certain expressions that we shall use. The starfish is given a bisymmetrical form by the madreporic plate, and the rays may be defined with reference to this plate. Placing the starfish with dorsal surface above and with the madreporic plate on that side of the disk which is next to the observer, the ray to the left of the plate will be called *a*, the next *b*, and so on to *e*, at the right of the madreporic plate. Figs. 10 and 11 give these designations in dorsal and ventral view; they will be found useful in following our descriptions of the reaction.

For brevity we shall often say that the starfish *uses* certain rays, as *a* and *b*, for turning itself; this will mean that it takes hold with these rays and turns on them,—the other rays swinging over. To say that the starfish "turns on," or "turns to-

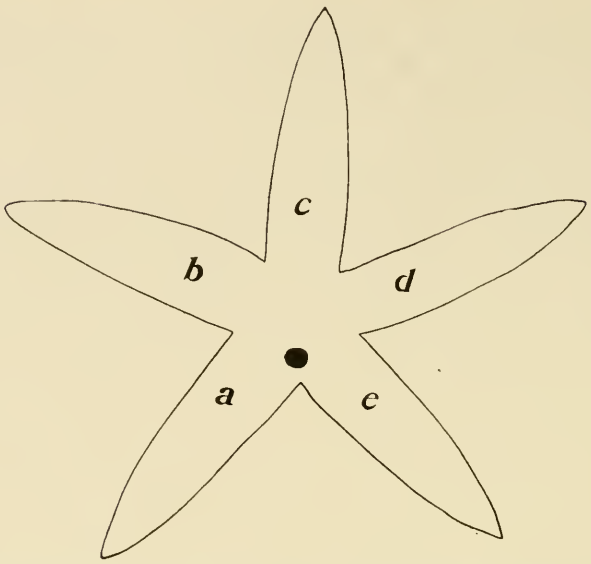


Fig. 10.—Outline of the dorsal surface of the starfish, showing the designation of the rays, as employed in the text. The dark spot is the madreporic plate.

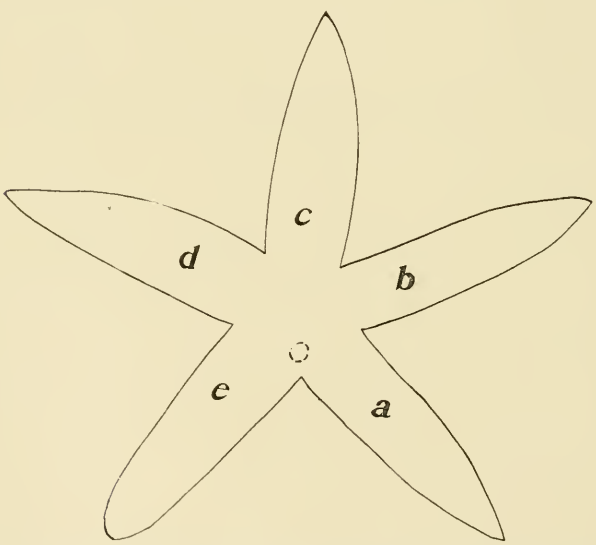


Fig. 11.—Designation of the rays as seen from the ventral surface. The position of the madreporic plate on the dorsal surface is seen in outline.

ward'' the rays *a* and *b* likewise signifies that these are the rays that attach themselves and pull the others over.

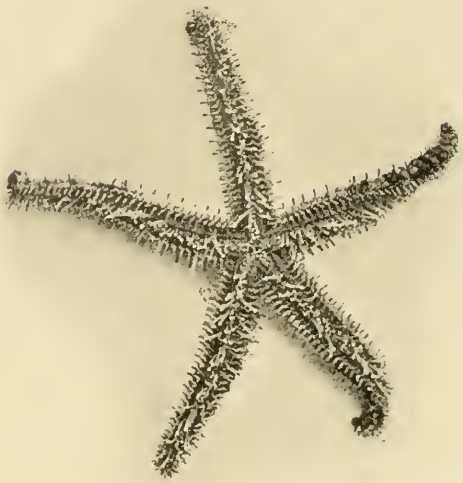
First, it may be said that my observations fully confirm Preyer's statement as to the variability of the righting reaction. It could probably be said, in a word, that the starfish may, and does, in different cases, right itself in any conceivable way,—and indeed, in many ways that would not readily be conceived before they were observed. But a mere statement of the fact of variability carries little insight. The variations may be grouped about a number of typical methods, and a statement of these with their modifications will give an insight into the nature of the reaction and the kind and extent of the variations.

The main types of the righting reaction, with the variations of each, are the following:

1. The simplest and neatest method of turning is the following: Two adjacent rays twist their tips in such a way that the ventral surfaces of the two face each other (fig. 12); then the tube feet of these rays attach themselves and throw the starfish over (fig. 13, 14, 15) in a neat somersault. Any two adjacent rays may act in this way, so that in a given starfish five different variations are possible.

2. The tips of the two adjacent rays may so twist that the ventral surfaces do not face each other, but both face in the same direction. The tube feet then take hold and throw the starfish over,—twisting it about an axis which passes lengthwise through one of the attached rays. This method of turning is extremely difficult and awkward, but is seen at times. Usually when two rays become attached in the way described, a third ray takes hold and aids the turning, the method then forming a transition to that given next. Any two of the rays may play the part we have described, so that there are five possible variations.

3. Three adjacent rays twist, attach themselves, and remain attached, all pulling throughout the reaction. Usually the animal turns primarily by the aid of the two outer rays, while the middle one is relatively passive, and is compelled to double back under as the animal turns. Often this middle ray walks backward beneath one of the other rays, or the other walks actively over its surface or there is a combination of these two movements, till



Figures 12 and 13.—The earliest stages of the righting reaction of the starfish. In Fig. 12 the two rays at the right have attached themselves in a co-ordinated way, but the unified impulse has not yet appeared; the tube feet of the different rays are extended in various directions. Figure 13 shows the conditions a little later; the co-ordinated impulse has appeared; all the tube feet are directed to the right, and all the activities of the starfish are henceforth devoted to turning in that direction.

Figs. 14 and 15.—Later stages in the righting reaction; photographs of different specimens.

the normal position is reached. (A model of the starfish, in paper or cloth, will make clear the necessity of such movements when three of the rays remain attached.) Five variants of this method are evidently possible, since any three adjacent rays may be used.

4. Four of the rays take hold, two extending to the right, two to the left. Then the fifth ray (which we may call the posterior one) is lifted straight up and swings directly over till its ventral surface reaches the bottom, while the anterior attached pair walks backward beneath the posterior attached pair, the latter walking forward over the surface of the latter. Nearly this type of turning is shown in progress in figs. 16 and 17. Five variants of this method are possible, depending on what arm is left free.

4. All of the rays attach themselves (figs. 18, 19). Now the turning can be accomplished only by the release of certain rays, when the method passes to one of the types already described.

5. An unusual method is that in which but one ray twists and attaches itself, and by its unaided efforts turns the starfish about an axis passing through this ray. This may be induced experimentally by preventing the other rays from taking hold; I have seen it occur spontaneously in a number of cases. Of course five variants of this type are possible, depending on which ray is used.

6. A still more unusual type is seen in the performance of the righting action without attachment of the tube feet of any of the rays. Preyer (1886) and Romanes (1885) have given accounts of certain ways in which this is sometimes accomplished. The typical method appears to be for the starfish to raise its disk high, standing on the tips of all the five rays, then to swing one or more rays over or one or more under, or both, until the body topples over, ventral side down. In my own observations the righting without attaching the tube feet was seen only when these were experimentally prevented from taking hold. The starfish then writhed and squirmed irregularly, taking various bizarre forms, until it had succeeded in getting its ventral side down, when the squirming ceased. No definable method was observable,—save that of making all sorts of movements till the end was reached.

As is apparent, each of these six methods admits of great

variation, even when carried out in the purely typical way. But to these must be added a very great proportion of irregular reactions, which may be classified as follows:

1. In methods 1, 2 and 3 the rays frequently become attached at first in such a way as to oppose each other's action,—one or more rays being twisted in the wrong direction for the way of turning that finally prevails. Examples of this are seen in figs. 16, 18 and 19. This complicates the reaction greatly. These wrongly attached rays either (1) release their hold entirely and are swung passively over by the other rays; or (2) they release, untwist, and take hold properly anew, again aiding in the pulling over; or (3) they untwist while still remaining attached, by a process of rotation on the long axis, "walking" by means of their tube feet; or (4) they remain attached until the righting is quite accomplished, becoming twisted 360 degrees; then untwist after the starfish as a whole has reached its normal position. Since any one or more arms may go through any of these maneuvers, the possibility of variation is extremely great.

2. A righting reaction that is begun by one method may be, and often is, finished by another. Four rays may work for a time; then one or two may release; or after one or two arms have initiated the turning, others may take hold and assist, or may modify the method. The animal may begin to turn in one direction; then change and turn in another. All sorts of combinations of the various possible methods occur.

Now, since it is clear that the phenomena we are studying are extremely variable, the next step is to discover, as far as possible, the causes of the variations. For every variation there must be some determining factor or factors; these must be worked out. Mere proof of the existence of variation and of its distribution does not, in any field, carry us far; it always constitutes essentially a plan for further work. Where the descriptive study of variation ends, physiological study of its causes begins. We wish to analyze the reaction, bringing out so far as possible the determining factors for every thing that occurs, and for the variations in different cases.

Let us begin our analysis by observing the first reactions of the starfish,—just what it does immediately after being turned over. Again we find much variation; we may classify as follows:

Fig. 16.—Righting reaction when four rays are attached.

Fig. 17.—Another righting reaction when four rays are attached, showing the crossing of one ray by another.

Fig. 18.—All five rays attached.

Fig. 19.—Irregular righting reaction.

1. Some starfish when placed on their backs (dorsal surface down, ventral surface up) at once lift *up* all their rays,—bending them toward the ventral side. The rays now wave about back and forth in the water, as if feeling for something. Then one or two begin to bend downward (dorsally), while at the same time they may begin to twist at the tip, so as to bring the ventral side below. Reaching the bottom, they attach and turn the starfish.

2. In other cases the first tendency seen is to bend all the arms downward (dorsally) instead of upward. Thus all quickly come in contact with the bottom; some or all twist and attach; some of the rays may rise and swing over and the starfish is turned.

3. Often at first some of the rays are lifted up (ventrally) and feel about, while others are bent down (dorsally), and twisted. The rays thus behaving differently may be variously distributed; the same ray may first bend downward, then before reaching bottom bend upward, or vice versa. The same ray may change its role several times before the method of turning is settled.

In all of the three types thus far mentioned, the rays which bend downward and attach may twist in various ways, so that they may not assist each other, or may even pull in opposite directions. Then there is likely to be some ineffectual pulling and hauling till certain rays untwist and change their method of action, and the righting finally occurs in a unified way.

4. Often when a starfish is turned on its back, there is evident an immediate *set* toward turning in a certain unified way,—a coördinated general impulse, appearing at once. Two of the rays, for example, will at once begin to bend downward (dorsally) and to twist in such a way as to take hold in a coördinate manner. At the same time the other three rays begin to rise up and go over, their tube feet all being directed from the beginning to the side toward which the turning is to occur; they are prepared as it were for meeting the bottom as soon as the turning is completed.

The Righting Impulse.—This unified, coördinated impulse toward turning in a definite way is perhaps the most striking and

is perhaps the most significant thing seen in the entire series of phenomena. As we have just seen, it is sometimes present at the beginning. In other cases it appears later during the reaction, but it is practically always evident before the righting is accomplished. Only in the first stages of the behavior is there opposition of action; then suddenly this unified impulse appears and all opposition and incoördination is gone. This unified impulse is clearly evident to the eye, and the precise moment of its appearance is apparent, through the peculiar action of the tube feet. So long as the different rays are not acting in unity, the tube feet are directed in all sorts of ways; the unattached ones of a given ray are likely to be extended in the direction in which that ray is trying to pull the starfish, while those of the central disk are extended directly upward. But suddenly all this changes; all the free tube feet incline in a certain direction; a visible unified impulse to turn toward a certain side appears at a stroke. This unified direction of the feet is shown in fig. 13, while in fig. 12 it has not yet appeared. Often at the moment this unified impulse appears, it is the only indication as to the direction toward which the starfish will turn, but it can be depended on to give a sure prediction as to the next move. As soon as it appears, the attached tube feet of those rays on the side toward which the starfish is to turn, which I may call the goal (the right in fig. 13), begin to pull with redoubled vigor, and the other tube feet of these rays extend out and take hold as rapidly as possible. The attached tube feet of the opposite rays (those of the *off* side, as we may call them) at the same time let go their hold and extend toward the goal (the side to which they are to swing), as if preparatory to meeting the bottom. In the intermediate rays, lying transversely, the tube feet participate in the coördinated movement in one of two ways. Sometimes they release their hold, extend toward the goal (or side toward which the turning is to occur), and allow the rays bearing them to be carried over in the general somersault. In other cases the tube feet of these transverse rays release on the off side and bend toward the goal. Those on the goal side retain their attachment, and new ones become attached on this side. All pull toward the goal, aiding the turning, and often causing these transverse rays to *walk* toward the goal side.

The observer at the appearance of this unified impulse is tempted to express the facts in an anthopomorphic way by saying that at that moment the starfish has decided which way to turn. The impression given is exactly that of the making of a decision, and there are few organisms, even among the highest, in which there are such clear outward signs of the moment when the decision is made[7].

After this impulse appears, all the activities of the starfish are directed toward turning in a certain definite way. Different rays and different tube feet play different roles; some attach, some release, some pull; certain rays walk under other rays; certain ones walk over the backs of others,—in fact, all the variations mentioned in our introductory classification are possible, though all are directed toward the same end. The impulse is *toward the performance of a certain complex act*,—namely, the righting reaction[8]. In view of the variations in method of performance, it seems impossible to express the nature of the impulse in any simpler way. The starfish reacts as a unit, not as a bundle of independent organs.

This unified impulse is perhaps the central fact in the righting reaction. In view of its existence, the remainder of our analysis centers about three questions:

1. What determines the varied actions of each part of the starfish before the impulse appears? Why does one ray twist and go down, another rise, etc., etc.?

2. How is the direction of the impulse determined? That is, how is it determined whether the starfish shall turn to the left, —toward the rays *a* and *b*, or toward *d* and *e*, or the like? How is it decided which rays shall play the role of attaching and pulling, which that of swinging over, etc.?

3. After the impulse has appeared, what determines the varied activities of the different parts? Why do certain tube feet now become released, others attached? Why do certain rays twist, others swing over without twisting; some walk in one

[7] I have given above an account of the typical cases. Sometimes the impulse is not so fully unified, and at times there is indecision; these important facts will be taken up later.

[8] As we have before seen, there is a similar coördinated impulse toward locomotion in a certain direction.

direction, some in another, some remain quiet for a time, then later begin to act, etc., etc.?

The first two questions are closely interconnected, and will be discussed mainly together. The third question is more independent, and will be taken up separately.

1. As to the first question, two general facts may be pointed out: (1) The action of the different rays before the impulse is set is sometimes determined by internal conditions, since they often show well-defined tendencies at the moment the animal is turned over. This has been set forth above (p. 132). (2) The action of the different rays is partly determined by external agents of various kinds. Both the internal and external factors are largely the same as those which determine the direction of the impulse, so that it will hardly be worth while to deal with them separately under each of these two heads. All the factors will then be considered under the next question.

2. *Direction of the Impulse.*—When the starfish is placed on its back, how is the direction of turning determined? We will take up separately the various factors involved.

(1) *Light.*—The direction of the rays of light plays a large part in determining the impulse. If the starfish is placed on its back near a window or other source of light, there is a marked tendency to turn, in righting, away from the lighted side. This factor is, however, only one of many, so that the results of experiments with light are of course not invariable.

Three specimens were placed before a brightly lighted window, and were each inverted on a plane level glass surface, ten times in succession. The animals were simply taken up and dropped on their backs, care being taken that there should be no constancy in the relation of given rays to the direction of the light. In the resulting thirty experiments, the starfish turned twenty times almost directly away from the window; four times obliquely away from the window, three times at right angles to the direction from which the light came, and three times directly toward the window.

In another series five specimens were used and each was given six trials, making again thirty experiments. In this series there were nineteen turns away from the window, three obliquely

away, five at right angles, one toward the window, and one in which the reaction was so complicated that its relation to the light could not be determined.

Thus, in sixty righting reactions, the turning was in thirty-nine cases almost directly away from the source of light, in seven cases obliquely away, in nine at right angles to the light, one intermediate, and in only four of the sixty cases toward the source of light.

It is therefore evident that direction of the source of light is an important factor in determining the impulse to turn. Often from the very beginning the two rays on the side away from the window bend down and twist over, preparatory to attaching, while those directed toward the window at once rise up and begin to go over. Light coming from one side may produce an immediate unified impulse and determine its direction. (After the impulse is established, as we shall see later, the direction of the light has little or no effect on the further course of the reaction.)

To test other factors, it is of course necessary to experiment under conditions in which the determining effect of light is excluded. This is readily done by placing the vessels containing the starfish in the bottom of a high cask or box, the light coming from above. Experiments now show that no particular direction of turning prevails.

(2) *Structural differences in the rays.*—Where certain rays are comparatively undeveloped, as when they are regenerating, these rays are little used in righting. The starfish attaches itself by the fully developed rays and turns toward these. In most starfish this factor plays little part,—though possibly invisible structural differentiations may at times play a role.

(3) *Rays that first come in contact with the bottom.*—When the starfish is placed on its back, it usually rests at first on its disk, the dorsal surface being convex. The rays, as we have seen, move up and down and feel about. It thus at times happens that certain rays come in contact (by their dorsal surfaces) with the bottom, before others do so. These rays are then likely to attach themselves by their tube feet, and to determine the direction of turning. A unified impulse appears,—the tube feet of the unattached rays inclining toward the attached ones.

This factor may play an important part, but it is by no means necessarily decisive. If the starfish is so deposited that the dorsal side of a certain pair of rays comes in contact first, the animals will usually turn in more cases toward these rays than in any other given direction. But there are many other factors that may determine the direction of turning in despite of this one. The direction of the light often overcomes the present factor. Indeed, any of the factors or combinations of factors to be mentioned may have this effect. In particular, it may be said that any factor which has determined the direction of the impulse before the dorsal surface of the rays has come in contact, will determine the direction of turning. Any factor, to act decisively, must come into action before the impulse is once set. After this, the direction of turning can be changed only with great difficulty.

(4) *Side of the rays that first come in contact.*—If the starfish is deposited in a tilted position, so that a certain side of a ray, or of two rays, touches the bottom first, then often all the tube feet of those rays incline at once toward that side, and tend to attach themselves. This is then followed by a similar action of the tube feet of all the rays; they incline toward that side (as in fig. 13). Thus a unified impulse has appeared. This factor is often overcome by others; it plays a part if it comes into action by itself at the moment when the impulse is to be determined.

(5) *Tilting of the body.*—If the starfish is placed on its back in a tilted position, one side being a little elevated, this may determine the direction of turning. This is because the tilting tends to cause the lower rays to come in contact first,—determining the direction of the impulse in the way mentioned in paragraphs (3) and (4). The mere inclination of the body in itself seems to be of no effect. In a large number of experiments the starfish was placed on plane surfaces inclined at various angles. There was no tendency to turn in righting with any special reference to the direction of inclination. The surfaces being plane, the rays were not more likely to touch sooner in one direction than another.

(6) *Contact with a small object.*—The starfish was placed

on its back, and a small object, as a pebble, was placed on the ventral surface of a ray. This was seized by the tube feet. In a certain starfish this determined five times in succession the direction of the turning,—the tube feet of all the rays at once inclining toward the object, so that the starfish turned in that direction. The pebble was placed in a different position in each case. In many other specimens such an object had no effect in determining the direction of turning.

(7) *Rays that first become attached by their tube feet.*—In many cases several or all of the rays come in contact by their dorsal surfaces with the bottom at about the same time. The tube feet of these rays then feel about, and some of them finally become attached. Up to this time the different rays have acted independently, each seeking for a hold. But as soon as the suckers of one or two rays are attached, one often sees all the other tube feet cease their irregular movements; they all incline toward the attached rays. The direction of the impulse has been determined, and the starfish now rights itself by turning toward the attached rays.

The action of this factor is often prevented or overcome by that of others. One frequently sees two rays become attached in a manner that would be most convenient for turning. Nevertheless, the other rays continue their searching, take hold, and may finally determine the turning,—the rays first attached being released. We shall later see certain reasons for this.

The rays that first come in contact with the bottom are of course likely, other things being equal, to be the first that become attached, so that factors (4) and (7) work together. But this is by no means always the case. Sometimes the rays that first come in contact do not find the bottom with their tube feet until after the later rays have done so. The result depends on the more or less independent activity of the rays and of the tube feet; both are variable.

(8) *Number of opposed rays that become attached.*—Sometimes on one side of the disk a single ray may be attached, on the opposite side two are attached, tending to turn the animal in the opposite direction from the first ray. In such cases, other things being equal, the side having fewer rays attached yields.

The single ray releases its suckers, and the animal turns by a unified impulse toward the other side. (It is not at all the case, as a rule, that the two rays by main force pull the opposed one from its attachment; all work together. Such a violent pulling away of a certain ray occurs in very rare cases, as will be mentioned later, but it is something quite out of the common.)

(9) *Relative number of tube feet that become attached in the different rays.*—Often some of the tube feet of all the rays, or of a number of rays that oppose each other, become attached before the unified impulse appears. Then, other things being equal, the direction of turning is determined by the relative number of tube feet attached. The rays having fewer tube feet yield, release their suckers, rise up, and turn toward the other side. Like any of the other factors, this one is often overcome by others. Frequently a starfish is seen to become well attached by one or two rays. Now another ray that has been waving about finds the bottom; its tube feet take hold one after another, and now the other rays yield, release, and turn toward the one later attached. There appears to be a predetermination of some sort in favor of the action of a certain ray, if it can but find a point of attachment. Indeed, as we shall see later, this is clearly the case.

(10) *Coördinated position and action of adjacent rays.*—The direction of turning is in some cases determined by the way that the tips of adjacent rays have twisted in becoming attached. There are three possible cases here: (*a*) The two adjacent rays may twist in opposite directions, so that their ventral surfaces face away from each other (as in the two rays to the right in fig. 18). Now the attached tube feet of the two rays of course pull against each other, so that it is impossible for the starfish to turn on these two rays, unless one or both untwist and take a new position. (*b*) The two adjacent rays may twist both in the same direction, so that the dorsal side of one faces the ventral side of the other. Turning on these two rays is then very difficult, involving a sort of whirling movement of the body; but it sometimes occurs. (*c*) The two adjacent rays may twist in such a way that their ventral sides face each other (fig. 13). This is the most favorable position for turning, the pulling of the at-

tached tube feet of these rays causing the starfish to turn a direct somersault.

Frequently the first pair of rays that become attached take the awkward first or second position. If now a second pair of rays becomes attached in the more favorable third position, then usually these determine the direction of turning. The ill-adjusted pair are released, and the animal turns on the pair that can pull in a coördinated way. Similarly, if two adjacent rays are first attached in one of the uncoördinated ways, another single ray may become attached in such a manner as to make a coördinated pair with one of the first two. Thereupon the starfish is likely to turn on this coördinated pair, releasing the third ray, or moving it merely in unison with the other two.

This factor, like all the others, is not always decisive. Often the direction of the impulse is determined by some other factor before the rays have become attached. Then lack of coördination in the rays may not change the direction; the starfish persists in its original direction, it turns awkwardly, twisting and untwisting the rays in various ways during the process.

Another conceivable factor should perhaps be mentioned here. Often when the starfish is resting on its ventral surface in the normal position, some of the rays lie close together, while others are far apart, with a wide angle between them. When such a starfish is turned on its back, it might apparently take hold and turn itself with the two rays that are wide apart, much more readily than in any other way. One might therefore anticipate that the direction of righting would be predetermined by the position of the starfish before it had been turned on its back. But experiments show that this is not the case. As soon as the starfish is turned on its back, its rays begin to wave back and forth, sideways as well as up and down, so that the original arrangement of the rays is quite lost before any of them become attached. The starfish is not more likely to turn on the two rays that were widely separated than on any others.

(11) *Experimentally releasing attached rays.*—The direction of turning may sometimes be determined in the following way: Three or four rays are attached, some tending to pull in one direction, some in the other,—the unified impulse not having

yet appeared. Now those rays which pull in a certain direction are forcibly detached from the bottom by the experimenter, whereupon the starfish begins to turn in the opposite direction, —a unified impulse appearing. (After the impulse has appeared, this releasing of certain rays has little influence, as we shall see later.)

(12) *Intense stimulation of certain rays.*—After several rays have become attached, some pulling in one direction, some in another, the direction of the impulse may often be determined by strongly stimulating certain rays, as by striking, pressing, or pinching them. Thereupon these rays begin to detach themselves, and the starfish turns toward the opposite side.

(13) *Impulse retained from a previous reaction.*—The direction of the impulse may have been determined in a given case by any of the methods mentioned above. The starfish is thus turning in a certain definite way toward a certain pair of rays. We now release it from its attachment, remove it to a new place, and place it in entirely different relations to the determining conditions. Nevertheless, it now turns just as it had begun to turn, toward the same pair of rays, the impulse once produced persisting in the new reaction in spite of changed conditions.

Again, the starfish may be allowed to finish righting itself, the direction of the impulse having been determined in any one of the ways described above. As soon as the righting is complete, the animal is turned anew on its back. *It now tends to right itself in the same way as in the previous case.* That is, the same rays are attached, the same ones go over; the turning takes place as before. The impulse determined in the previous reaction persists through the second reaction.

Thus in this second reaction the direction of turning is not determined by any present external factor whatsoever, but by a persisting internal disposition to turn in a certain way—to use certain rays in certain roles. We shall give further details of this persistence of the impulse in our general discussion of the impulse and its nature (p. 145); here we are merely enumerating the factors on which, in different cases, the righting reaction is found empirically to depend.

(14) *Impulse present at the time the animal is turned.*—At

times when a starfish is turned on its back, it is found to have at the beginning a definite *set* toward turning in a certain way (see p. 132). The unified impulse is present at the beginning: certain rays bend down, twist, take hold of the bottom and pull, while others rise up and go over. There is no hesitation or wavering in the role to be played by each part, from start to finish. This is sometimes found to be the case even with a starfish that has not been under experimentation before, so that the direction of the impulse has not been determined in the way described under (13). There are doubtless other ways in which a persistent tendency toward a certain direction of turning may be determined before the animal is placed on its back. It is possible that the direction of locomotion just before the starfish is turned may act as such a determining factor. It would not be surprising if it should be found that the starfish tends to turn toward those rays which were moving in advance at the time the animal was inverted. I regret that I did not test this by experimentation; it did not occur to me as a possible factor till I had left the shore.

(15) *Permanent tendency to turn toward a certain pair of rays.*—Will repeated experiments on the same starfish show a tendency to turn in any definite way? This question was studied in a number of specimens. They were allowed to turn at intervals of several minutes on a plane surface, in diffused light, so that the external factors were made as nearly uniform as possible. Moreover, the position was varied in different experiments so that the rays of a given starfish had different relations in each case to the surroundings. The results of these experiments are given in the following. Since in most cases a starfish turned by using a certain pair of rays to attach and turn itself, while the other three arms were merely raised and went over, the method of righting can be given by specifying the two rays that were thus employed. Thus, if in a given case the starfish attached itself by the rays *a* and *b* (fig. 10), and pulled itself over by their aid, the record simply states that it "turned on *a* and *b*," or that "*a* and *b* were used." If there were no predilection in favor of certain rays, we should expect each to be used an approximately equal number of times.

The actual results are as follows:

Starfish A.—Twenty experiments. Rays used: *e*, 17 times; *a*, 15; *c*, 4; *d*, 3; *b*, 1.

Combinations of adjacent rays used: $a + e$, 12 times; $c + d$, 2; $a + b$, 1; $d + e$, 1.

Ten experiments three days later. Rays used: *e*, 8; *d*, 8; *a*, 3; *b*, 1; *c*, 1.

Combinations of adjacent rays: $d + e$, 6; $a + e$, 2; $a + b$, 1; $c + d$, 1.

Totals of the thirty experiments: Rays used: *e*, 25; *a*, 18; *d*, 11; *c*, 5; *b*, 2.

Combinations used: $a + e$, 14; $d + e$, 7; $c + d$, 3; $a + b$, 1; $b + c$, 0.

There is thus in the starfish *A* a strong tendency to use the ray *e*, this being employed twenty-five times out of a possible thirty. The ray *b*, on the other hand, is discriminated against; it attached and pulled only twice out of the possible 30. Of the pairs of adjacent rays, a + e is used in nearly half of all cases, while $b + c$ is never used.

Starfish B.—Fifteen experiments. Rays used: *a*, 15; *e*, 14; *b*, 1; *d*, 5 times as a third subordinate ray in connection with $a + e$; *c*, 0.

Combinations of adjacent rays: $a + e$, 14; $a + b$, 1. The rays a + e were accompanied in five cases by *d*, which attached itself, but was mainly passive.

Ten additional experiments three days later. Rays used: *a*, 7; *e*, 4; *b*, 3; *c*, 3; *d*, 2.

Combinations of adjacent rays: $a + b$, 2; $a + e$, 1. The other reactions were performed with two *non-adjacent* rays in action, —a ray between them being passive.

Total of the twenty-five experiments: Rays used: *a*, 22; *e*, 18; *d*, 7; *b*, 4; *c*, 3.

Combinations of adjacent rays: $a + e$, 15; $a + b$, 3; $b + c$, 0; $c + d$, 0; $d + e$, 0.

Here again we see a strong tendency to use the rays *a* and *e* in preference to others.

Starfish C.—Ten experiments. Rays used: *e*, 5; *d*, 4; *a*, 3; *b*, 3; *c*, 1.

Combinations used: $a + b$, 3; $d + e$, 2. The rays *d* and *c* were each employed quite alone in two reactions.

Thus *e* was used in half of all the reactions.

Starfish D.—Ten experiments. Rays used: *d*, 10; *e*, 9; *c*, 1; *a*, 0; *b*, 0.

Combinations used: $d + e$, 9; $d + c$, 1.

Thus there is here a strong predilection for the combination $d + e$.

Starfish F.—Ten experiments. Rays used: *e*, 8; *d*, 4; *c*, 4; *a*, 3; *b*, 0.

Combinations: $e + d$, 2; $a + e$, 1.

Starfish G.—Ten experiments. Rays used: *e*, 8; *a*, 4; *b*, 3; *c*, 2.

Combinations: $a + e$, 2; $e + d$, 2; $a + b$, 1.

Starfish H.—Ten experiments. Rays used: *e*, 6; *a*, 6; *d*, 4; *b*, 2; *c*, 2.

Combinations: $d + e$, 1; $c + d$, 1; $b + c$, 1.

Summary of the ninety-five experiments given above:

Rays used for pulling starfish over: *e*, 89; *a*, 56; *d*, 43; *c*, 18; *b*, 14.

Combinations of adjacent rays used: $a + e$, 37; $d + e$, 27; $a + b$, 9; $c + d$, 3; $b + c$, 0.

These results show clearly two things:

1. Individual starfish do have a more or less permanent "set" toward the use of certain rays in pulling themselves over in the righting reaction. In the starfish *A* and *B*, the preference is for the pair $a + e$; in *D*, for the pair $d + e$. In *G* and *H* no one combination has so marked a preference, but the rays *a* and *e* are used more than any others. In *F* we can only say that there is a marked preference for *e*.

2. There is for some reason a general tendency, seen in all the specimens, to use certain definite rays for the pulling over. A strong tendency is evident toward using the rays lying close to the madreporic plate. The ray *e* is used 89 times out of the 95, and the next greatest numbers are shown by the two rays lying on either side of *e*, namely *a* (56) and *d* (43). The combination of the two rays lying at the sides of the madreporic plate ($a + e$), was used 37 times. On the other hand, the rays lying opposite (*b* and *c*) were used but rarely, and *not once in the whole 95 experiments was this pair* $b + c$ *used in combination.*

What is the explanation of these facts? Two possible factors suggest themselves. (1) The permanent *set* of a given individual might be partly due to *habit*, resulting from the repetition of certain reaction methods in the past. This possibility will be treated in the next section. (2) The fact that there is a strong preference in all the cases for the use of the rays next the madreporic plate suggests that there are permanent structural or functional peculiarities found in the starfish, which tend to cause the preference for certain rays. The very great preponderance of the use of the rays *c* and *a* in our 95 experiments indicates that such peculiarities exist, though they allow a very great latitude for the play of other factors.

Summary on the Righting Impulse and on the Factors Determining it.—The foregoing account shows that the number of different factors which may determine the righting impulse is great. The general result may be summed up as follows: When the starfish is placed on its back, this throws the animal as it were into a state of instability, shown in its varied movements, and prepares it to take an impulse toward turning in one direction or another. In this unstable condition any one of a great number of factors may determine the direction of the impulse. In general, whatever factor comes into action first determines the impulse. This factor may be any one of a large number of external conditions, or it may be an internal condition.

Persistence of the Impulse.—While the direction of the impulse is thus easily determined when the animal is in the condition of instability, it is not easily changed after the impulse is once established. The same factors that at first determine its direction with the greatest ease are quite without effect after the determination is once made. The impulse persists most obstinately after it is once formed, in spite of changing conditions. This is shown in all the experiments.

Thus a starfish is placed on its back with the light coming from the right. Thereupon the animal shows an immediate impulse to turn to the left (away from the light), on the left-hand rays *a* - *b*, we may say. As soon as this impulse is evident, from the inclination of the tube feet toward *a* - *b*, we turn the vessel around, so that the light comes from the side *a* - *b*. Turning

on these rays will now cause the starfish to turn directly toward the light. Yet it continues to turn on these rays *a* - *b*. The direction of the light having once determined the impulse, a change in its direction has no effect.

This persistence is seen even if the starfish is turned around before any of the tube feet or rays have attached themselves. It is only necessary that the unified impulse toward turning in a certain way shall have appeared, in the inclination of the tube feet. Again, if after the starfish has partly attached itself and has begun to turn in a certain direction, we forcibly release it from its attachment and place it under quite new relations to the outer conditions, it resumes, when again placed on the bottom, its original way of righting, turning on that pair of rays on which it had begun to turn.

This persistence of the impulse is very marked in experiments in which an attempt is made to change the impulse so as to cause the formation of new habits, as described in the next section. Thus, after the starfish has taken hold with a certain pair of rays, if we forcibly release these from their attachment, the animal frequently simply attaches them again, and continues to turn as before. If not too great violence is used, sometimes a given pair of rays may be detached half a dozen times in succession without causing other rays to take hold, or any change in the direction of the impulse. In certain cases the starfish had taken an impulse to turn on a certain pair of rays, *a* and *e*. Releasing both of these, the animal continued its efforts to turn in that direction. The two rays were forcibly prevented from becoming attached, but the animal refused to take hold with the other rays and made repeated efforts to bring *a* and *e* in contact again. Finally, in spite of my efforts to prevent, it managed to take hold with *a*, though I managed to keep *e* from getting hold. But now the starfish turned just as it would have done if both were attached, the unaided efforts of *a* pulling it over in the usual way.

Changing an Established Impulse.—Yet of course the impulse is sometimes changed after it is once established. Different starfish differ greatly in the ease with which the direction of the impulse can be changed. Some specimens are extremely

"obstinate," persisting in turning in a certain way in spite of all sorts of opposition. In others the direction of the impulse is changed much more readily. Sometimes when the attached rays are forcibly released, the direction of the impulse at once changes, though this is not usually the case. The strength of the impulse varies even in the same individual. If the direction of the impulse has been changed several times by outside interference, it often after a time becomes strongly set, and is no longer influenced by the conditions which at first changed it.

It seems to be a general rule that the impulse is not so firmly set when it is first formed, as later. Often when a starfish is turned on its back, a common impulse appears after a short period of uncoördinated struggling; all the tube feet turn toward a certain side. Suddenly this impulse is seen to change, all the tube feet inclining in a different direction, and the starfish beginning to turn that way. The impulse may often be changed with great readiness in this period immediately after it is formed, by stimulating certain rays, or the like. But again, in some cases the impulse is strongly set at the beginning, and can not be changed without strong and repeated stimulation.

A formed impulse may usually be caused to disappear by lifting the starfish from the bottom and holding it suspended in the water, back downward, a minute or two. At first it usually attempts to continue turning in the way already begun. But its tube feet and rays not coming in contact with anything, it soon gives this up; the coördinated impulse disappears, and all the rays and tube feet begin to feel about in various directions. A new impulse may then be determined by some object with which a certain ray comes in contact.

Indecision.—Since there are so many factors any one of which may determine the direction of the impulse if it acts at the moment of instability, there is of course little chance that the direction of turning will be left long undecided. Yet there are often a few moments of uncertainty, and in rare cases the factors tending to cause turning in opposite directions are so evenly balanced that a more prolonged period of indecision results.

During the moments before the unified impulse appears, often several rays have attached themselves and are pulling against one another. Now the unattached tube feet show great diversity of action. Those of a given ray stretch out in the direction in which the attached ones of that ray are pulling, so that there is a sort of partial unity of impulse for the single ray. In an unattached ray the tube feet point usually in the direction pulled by the nearest attached ray. If two rays near by are pulling in different directions, often the tube feet of the unattached rays, or of the disk, stretch out first toward one side, then toward the other.

This state of indecision usually lasts but a short time; but sometimes it is prolonged. Thus, in a certain case, one ray (*c*) did not attach itself, while the other two pairs became attached in a symmetrical way on its right and left. These four rays became attached nearly simultaneously, and about the same number of tube feet were holding on each. There was thus little to determine an impulse to one side rather than the other, so that the starfish remained for several minutes on its back, the rays vainly pulling against one another. Sometimes all the five rays become attached and pull against each other for several minutes in the same way. As might be expected from the great variety of factors which may determine the impulse, the state of indecision never lasts indefinitely; finally the unified impulse appears; certain rays release their hold and allow themselves to be pulled over by the attached rays.

Further account of the unified impulse is reserved till we have investigated habit formation, since the latter throws much light on the determination of the impulse.

Formation of Habits in the Starfish.

We have seen above that when the starfish begins to act in a certain way, it persists in that action for some time, even in spite of opposing conditions. Furthermore, we have seen that individual starfish have a more or less permanent "set" toward acting in certain ways,—toward using certain rays in one manner, others in another, in the righting reaction and the like. These facts naturally suggest the possibility that the starfish

forms habits, and that these set tendencies are due to habits previously formed. To investigate whether this is true is the purpose of the present section.

The formation of lasting habits has been demonstrated among lower animals in the *Crustacea* (Yerkes, Spaulding), in annelids (Mrs. Yerkes, 1907), and in flatworms (Bohn)[9]. All these animals have the nervous system so centralized that one or more important ganglia can be distinguished, the largest of which is commonly called a "brain." In the starfish there is no such centralization of the nervous system. There is a nerve cord which forms a ring about the mouth, and from the five angles of this ring nerve cords run outward in each ray. Besides these parts there are fine networks of nerve fibers over the surface and among the tissues. The ganglion cells are scattered in the cords and nets, along with the fibers; there is no concentration anywhere into ganglia.

It has never been shown that animals with so simple a type of nervous system can form habits[10]. Whether the possibility of habit-formation depends on a certain complexity of the nervous system is a matter of much interest. Furthermore the general question of the distribution of the power of habit-formation is one of great importance. I have, therefore, attempted to test this matter in the starfish with great care.

By the word *habit* there is commonly understood a *lasting* modification of behavior due to experience. In taking up the question of habit formation, one is compelled to deal at the same time with modifications of behavior that may show themselves only for a short period. There appears to be no precise term for designating these, though their acquirement is often spoken of as *learning by experience,* or as a manifestation of *intelligence,*—both expressions having a somewhat subjective tinge that it is desirable to avoid in an objective investigation. It will, perhaps, be impossible to avoid them completely, but the word *habit* may be stretched a little, so that we may designate these non-permanent modifications as temporary habits. If after being trained to right itself in a certain way, the starfish should

[9] See the review of this matter in my book on the *Behavior of the Lower Organisms*, pp. 254-259 (1906).

[10] Certain statements of Preyer on this matter will be taken up later.

tend to spontaneously right itself in that manner for, say, half an hour, this would be an example of what is meant by a temporary habit.

Preyer (1886) has given in his valuable paper on the movements of the starfish certain observations which might bear upon habit-formation. He tried placing specimens of the starfish on a smooth hemispherical surface, from which it would be as easy to crawl in one direction as another, in order to determine whether the animals prefer moving with any particular ray in advance. The general result of many varied experiments, with many specimens, was that no particular ray was preferred above others. But in repeated experiments with single individuals, he found in several cases that the given individual showed a marked preference for movement with a certain ray in advance. Thus, a specimen of *Astropecten pentacanthus* moved with the ray 4 (ray *d*, fig. 10) in advance fifteen times out of a series of twenty experiments. Such results suggest the possibility that the preference is due to habit,—though this possibility was not mentioned by Preyer. I endeavored to determine experimentally whether such a habit could be formed. Starfish were placed in such a situation as that described by Preyer, then the tips of one or two rays were strongly stimulated, in order to compel the starfish to move toward the opposite side. By thus compelling the animal to move many times with a certain ray in advance, it was thought possible that a habit might be established, so that the starfish would move with that ray in advance even when not compelled to do so. But unfortunately I found it impossible to drive the starfish in a certain direction. When the tips of certain rays were strongly stimulated, the animal, instead of fleeing, in nine cases out of ten merely contracted its tube feet strongly, so as to shrink close against the surface and cling tightly there. This test for habit-formation was therefore abandoned.

In certain other experiments Preyer gives a statement of results which if confirmed would amount directly to temporary habit-formation, or to "learning by experience." He tried to confine the starfish by means of large flat-headed pins, placed in the angles between the rays, close to the disk, and driven into the board on which the starfish lay. The animals tried by

various methods to escape, taking much time and making many movements of the most varied character before they were finally successful. According to Preyer, when the experiment is repeated several times on the same individual, the time required for escape becomes less, and the number of useless motions performed is likewise decreased. The starfish has thus improved through experience; it might be said to have "learned" how to escape; or it has formed the habit of escaping in a certain way. But Preyer gives no precise data on this matter, as to the time or the number of movements used; his statement is evidently based merely on a general impression. As we shall soon see, later work has not substantiated these results, in the case of starfish left to work out for themselves a method of action.

Preyer (*l. c.*) described certain other experiments, on the brittle star, the results of which were of such a character that Preyer characterized the starfish as "intelligent." These experiments are of much interest in themselves, and they formed the basis for the later work of Glaser (1907), immediately to be mentioned. It will, therefore, be worth while to take them up briefly, the more so since Preyer's results have been called in question by Loeb. It will be of interest further to determine just what were Preyer's grounds for attributing intelligence to the brittle-star. Preyer slipped a short rubber tube over one of the rays of the animals to its base. He found that this caused the creature to perform many varied movements till by one of them the tube was removed[11]. Among the methods described by Preyer for removing the tube, there are certain ones which look like a definite attempt toward accomplishing this end. Thus, the animal, after dragging behind it for a time the arm bearing the tube, stopped, placed another arm against the tube, and pushed it off, the spines along the sides of the arm serving to give it a hold on the tube. Sometimes one of the adjacent arms was used in this way, sometimes two. In another case, where the tube covered the stump of an arm, the animal placed this stump bearing the tube against the side of the disk and strongly rubbed. This displaced the tube a little, but it still remained

[11] Preyer's experiments were performed on species of *Ophiomyxa* and *Ophioderma,* from the Bay of Naples.

attached. Now one of the other arms was placed on the tube and it was thus held down against the bottom, while the stump of the arm was pulled out of it.

These interesting facts have been called in question by Loeb. He says "I have repeated the experiment on these animals and found that the *Ophiuris* pays no attention to the rubber tube. The animal of course loses it after a time unless it fits too closely, but it is always purely a matter of chance" (Loeb, 1900, p. 65). It is, therefore, proper to point out that Preyer's facts have been essentially confirmed by later investigators. V. Uexküll (1904) gives a series of kinetographic photographs of the brittle star while engaged with the adjacent rays in the scratching movements ("Kratzbewegungen") by which the tube was finally removed. Glaser (1907) described similar actions. I performed the same experiment with a species of *Ophiuris* (*O. panamensis* Lütken) with similar results. I observed in the course of my experiments all but one of the five different methods of getting rid of the tube which Preyer described. In one case the two adjacent arms were placed against the tube in the way figured by Preyer, pushed out in such a way as tended to remove the tube; drawn back and again placed against the tube and pushed outward, and this was repeated six times in succession.

Of course not *all* the specimens on which this experiment is tried proceed in the same way in removing the tube, nor does the same one behave in the same way at all times; this was specially emphasized by Preyer. The denial of such observations is likely to come from investigators who are fully convinced of the truth of the ancient dogma that the behavior of the lower animals is stereotyped and invariable. Holding to this view, one or two 'crucial experiments' are deemed all that is necessary to set the matter at rest. When the established truth that the behavior of the lower organisms is specially characterized by variability and changeability is generally recognized, we shall have fewer dogmatic statements as to the precise limitations of these animals and as to what they are *forced* to do under certain outward conditions.

Why did Preyer call this behavior "intelligent"? In the case of such thorough workers as Preyer, we are likely to gain

a better insight into the problem by inquiring as to just what phenomena formed the basis of this idea, than by merely crying out against anthropomorphism, or by showing on the basis of definitions made since the time of the author in question, that he is wrong. Preyer's view that the brittle star shows intelligence in this behavior is evidently due to the fact that the animal does not move at random, but sets to work by such a combination of activities as is actually well fitted to remove the source of irritation. Preyer could therefore argue that the action requires something like an understanding of the relation of means to end, and this indeed in a somewhat complicated combination; this (he would say) *requires* intelligence. Preyer would be further confirmed in this view by the fact that when one of these well-directed combinations of movements is not successful, another is tried.

To Preyer's characterization of this behavior as intelligent, of course the objection can very properly be made that it does not fulfill the objective definition or test for intelligent action that is now commonly accepted (see Glaser, 1907). But this does not do away with the actual problem which Preyer had in mind,—namely, how does the brittle-star happen to be able to make so *purposive* a combination of movements, in circumstances that required it? This seems to require at least something like what Driesch (1903) has more recently characterized as "objective knowledge". A similar problem comes up in connection with the righting reaction, and it will there be more fully discussed (see p. 173). The older investigators would probably have maintained that the use of these purposive combinations of movements (in cases that clearly do not come under the accepted definition of *instinct*), requires that they should have been reached by such adaptive modifications as would come clearly under even the modern objective definition of intelligence.

But of course it will not do to abandon the direct experimental test for adaptive modifiability and Glaser (1907) has recently repeated these experiments of Preyer to see if such modification can be demonstrated. He repeated the experiment with the rubber tube many times on the same individual, to see whether it would improve in removing the tube,—either by

shortening the time required, or by adopting better methods in later tests. Glaser found that there was no improvement; the later tests require as much time, and involve as many varied movements as the first ones. In the same way Glaser finds that there is no improvement in many trials in the righting reaction of the brittle star. After righting itself many times, the animal requires as much time and employs as many movements as at first. Glaser therefore concludes that the brittle-star shows in these experiments no indication of intelligence.

In these experiments of Glaser the animal is of course left to itself while "solving the problem", the object being to discover whether it will of itself under natural conditions "improve" in the performance of a complex act in consequence of repetition; the results are negative. I carried on a considerable series of experiments of the same sort, my results confirming throughout those of Glaser. I first tried Preyer's experiment of fastening the starfish by means of broad-headed tacks placed in the angles of the rays (see p. 150). I found, as Preyer had done, that the animal under these conditions performs many movements of most varied character, and that by one or the other of these it always finally escapes. But in a long series I was unable to confirm Preyer's statement that there is improvement in a given individual after it has been repeatedly subjected to the experiment. The length of time required to escape does not decrease, nor is there a decrease in the number and variety of the movements before escape is effected. The starfish does not discover that one method accomplishes the result more readily than another, and thereafter use that method.

In the same way I kept precise records in a long series of experiments on the righting reaction. After repeated experiences by a given individual, there was no improvement in the performance of this reaction, either in the time taken, or in the number of movements employed in accomplishing the righting.

Thus my results so far confirm throughout those of Glaser. When left to themselves, these animals do not, as a rule, improve, nor form habits as a result of the repetition of a complex act.

As Glaser well points out, this negative result may be due, not to any actual incapacity for habit-formation, but to what

may be called the remarkable versatility of the starfish. This animal may do in an indefinite number of different ways anything that it may do at all. Its locomotion is an excellent type of its entire behavior in this respect. The starfish is not hampered by any considerations of anterior and posterior; it may move with any one of its rays in the lead, or with any interradius in advance, or indeed in any intermediate direction, so that its possibilities as to variations of direction of locomotion are really unlimited. In the same way, as we have seen in detail, it may right itself in an indefinite number of different ways. It shows the same versatility when confronted with such a problem as the removal of the rubber tube placed on its arm, or the escape from confinement by tacks. It may and does solve these problems in any one of many different ways; almost any method which it adopts proving effective in the long run. Under these conditions it is evident that there is little occasion for adopting any particular method as a habit, even if habit-formation is possible.[12]

Conditions Required for Habit-Formation.—These facts lead to a careful consideration of just what conditions are required for habit-formation. These appear to be the following: (1) The organism must be presented with a situation or "problem" that shall cause it to react and to continue reacting till the situation is essentially changed,—the problem "solved". (2) The organism must react in several different ways; it must "try" to "solve the problem" in more than one manner. (3) It must be able to solve the problem or relieve the situation in only one, or at least in only a limited number, of these ways. If this third condition is not fulfilled, there is no strong ground for any special method being selected, and so for the formation of a habit. If any method will work, none is specially preferable.

It is not easy to devise "problems" fulfilling all these requirements, for organisms with which we have so little in common as with the starfish or with other animals in a corresponding low position in the scale of development. The problems thus far

[12] These considerations on the "versatility" of the starfish forced upon one by the results of an experimental investigation, are interesting in view of the old idea that the reactions of such lower animals are fixed and unvarying. The behavior of lower organisms differs from that of higher ones, rather in its great indefiniteness and inconstancy.

mentioned have fulfilled the first two requirements, but not the third one.

Method of training the Starfish.—It occurred to me that the difficulty might perhaps be met by interfering directly and continuously in the course of the reaction and preventing the starfish from succeeding save by one method. For this the righting reaction was selected. The starfish was placed on its back, then, by holding the rays with the hands or forceps, releasing them from their attachment, etc., etc., the starfish was prevented from turning save on a certain pair of rays. The starfish was, as it were, *trained* to turn on a certain pair of rays.

It needs to be pointed out that this "training" does not imply anything different in principle from what is found in nature; there is nothing "artificial" about its results. The starfish merely finds in the course of its reaction that it can right itself in only one way, so that we are able to test whether this will result in habit-formation. It is clear that the same results would be attained if this effect were produced in any other way than by the use of the human hand, and conditions might readily arise in nature that would have the same action.

Experiments in Training the Starfish.

A thorough, extended course of training was given to but two individuals, while three others were worked with for a shorter period and in a less thorough way. The effect of a brief series of "lessons" was, however, tested on many other individuals. The small number of individuals employed in extended and thorough work was due to the very great amount of time required in the experiments, and to the fact that the successful method of work was not hit upon till near the end of the season. A given starfish may require two to seven minutes for its reaction, and the careful description to be written requires still more time. Then there is the period of rest between successive lessons. Altogether, by the time five specimens have been given ten lessons, at intervals, the part of the day left for other work is small. Moreover, the work is extremely tedious to the experimenter, so that it is almost necessary to vary it with work of a different character,—especially in view of the fact

that, in these first series of experiments, it was uncertain whether the results might not be thoroughly negative, and the work practically thrown away.

Our problem is, to train the starfish when righting itself to use a certain pair of rays with which to grasp the bottom and pull itself over. The rays thus "used" are those employed like the pair to the right in fig. 13. (Of course all the rays are *used* in one way or another; we shall confine attention to those used for attaching and pulling over.)

It is first necessary, of course, to determine whether the animal has any predilection for the use of certain rays before training is begun. This, as we have already seen (p. 144), is actually the case. Of 95 experiments with a number of specimens, the ray *e* was used 89 times, the ray *b* but fourteen times. Out of the 76 cases in which a definite pair of adjacent rays were employed, a pair containing *e* was used 64 times, $a + e$, 37 times; $d + e$, 27 times. On the other hand, the pair $b + c$ was not used once in the entire 95 experiments.

Thus in endeavoring to train the starfish to turn on a certain pair of rays, it will be necessary to avoid $a + e$ and $e + d$, and to select some pair on which the animal has no previous tendency to turn. Selection of the pair $b + c$ will evidently present the most difficult test.

I shall give a rather full account of the methods and results in the case of the two starfish that were under training for a long period, as this will bring out many essential points.

Starfish "A."—The first individual with which I worked I called starfish "A." Thirty test experiments with this individual showed, as we have seen on page 143, a strong tendency to use the rays *e* and *a* in the active work of turning, *e* being employed in 25 cases, *a* in 18 cases. The precise combination $a + e$ did the active work in 15 out of the thirty cases. On the other hand, there was a strong disinclination to use the rays *b* and *c*; *b* was employed but twice and *c* only 5 times in the thirty experiments, while the pair $b + c$ was never used in combination.

Will it be possible to train the starfish to employ by preference this combination $b + c$, which it never uses before training? Experiments with this in view were begun July 21, 1906.

The starfish was placed on its back. The rays and tube feet began to twist and endeavor to take hold, but this was prevented in the rays *a*, *d* and *e*, by stimulating their tube feet with a glass rod whenever they tried to attach themselves,—so that only the rays *b* and *c* were able to take hold. Ten experiments were performed in series, with intervals of two minutes between them. As the first few experiments are very instructive, they will be described in detail.

1. The first experiments showed strongly the tendency of *b* to rise up and go over in place of twisting, attaching itself, and pulling. In experiment 1, though *b* and *c* were the only rays permitted to attach themselves, *b* obstinately refused to do so, and persisted in rising and attempting to swing over in the usual way. After some delay, *c* attached itself and turned the starfish unaided,—*b* consistently refusing to play any part but its usual one.

2. In the second experiment I restrained all the rays except *b* from attaching themselves. After much threshing about, *b* finally came in contact with the bottom and took hold. Then *c* was allowed to assist, and the two turned the starfish.

3. This time *b* and *c* were left equally free to act, whereupon *c* turned the animal unaided,—*b* again refusing to attach itself.

In the next experiments my efforts were concentrated on *b*, in an attempt to overcome its refusal to attach and pull.

4. In the fourth experiment I again prevented the attachment of all rays but *b*. But the latter persisted in rising, waving about, and endeavoring to swing over in its usual way. All the other rays made repeated attempts to attach themselves, which I prevented. But the animal kept twisting and squirming about until finally it managed to swing *b* over in the usual way,—so that by perseverance it had managed to right itself without attaching any of its rays.

5. Again *b* was obstinate, but all the other rays were prevented from attaching, and finally in the course of its squirming *b* accidentally came against the bottom. This, as in experiment 2, seemed to operate as a stimulus to cause the disposition of *b* to change; it now attached itself. In order to give *b* practice in doing the active work of turning, I still prevented all the

other rays from attaching, so that *b* pulled the starfish over alone.

6. This time *b* was forced to take hold, as in the last experiment, by preventing other rays from attaching till *b* had come against the bottom. But this time, as soon as *b* was well attached, I allowed the other rays their freedom. At once these attached themselves; *b* released its hold, and swung freely over in the usual way,—the turning being mainly done, as usual, by $a + e$.

7. Prevented others, till *b* was attached. Then others took hold. This time *b* kept its hold, but did almost nothing to aid the turning, which was mainly brought about by *a*.

8. By preventing others, *b* finally driven to attach itself and turn the starfish unassisted.

9. Again *b* was driven to take hold, by preventing the others. This time *b* attached itself much more readily than before, taking hold as soon as it was evident that the other rays could not do so.

10. In the tenth experiment *b* attached itself almost at once, as soon as the others were prevented.

Thus these ten lessons of the first day had to be devoted mainly to overcoming the obstinate refusal of *b* to attach itself. The ninth and tenth experiments seemed to show that the training was having some effect, *b* acting more readily than before, though still with reluctance.

In the ten lessons of the second day, the training was again directed toward both *b* and *c*, by preventing the other rays from attaching. At first *b* showed the same disinclination to attach itself, as before; in the first experiment *c* did the turning alone. The ray *c* in all these experiments made persistent efforts to attach itself, seeming as strongly bent on playing this role as *b* was on playing the opposite role. In experiments 2-5, *b* and *c* after a time took hold and turned the starfish. But these two rays worked very awkwardly together; they usually twisted their tips in opposite directions, so that even after they were attached they were unable to turn the starfish. After they had struggled for a time, there was a strong tendency for *a* to take hold, in such a way as to coöperate with *b*; this occurred in spite of my efforts to prevent it, in several of the experiments. It is clear that it would be much easier to induce $a + b$ to do the turning,

than $b + c$, owing to the lack of coördination in the twisting of the latter.

In experiments 5 to 8, *b* took hold readily, its original disinclination seeming to be quite conquered; it was usually attached and began pulling before *c* had done so. Indeed, *b* was almost the first of the rays to bend back, twist, and endeavor to attach itself. The ray *e*, however, continued to make active efforts to attach itself, as it did at first.

Now, after these eighteen training lessons (ten the first day, eight the second), which had been directed mainly toward inducing *b* to play the part of attaching and pulling, the starfish was allowed to right itself five times in succession without any interference or assistance (there being but the usual two minutes between the last of the "lessons" and the series of free reactions). In every case the ray *b* at once began to bend down, twist over, and attach itself; it was the first ray to take hold in most of the five free experiments. In the first of the free trials this ray *b* turned the starfish practically unaided, though when the turning was nearly finished the ray *e* took hold and helped a little. In the succeeding four free trials the work was done by *b* and *e* in common. In one case *e* became attached first, but *b* persisted, took hold also, and played an equal part in accomplishing the reaction.

Thus in this starfish A the method of turning had been completely changed by a course of eighteen lessons of training. Before the training *b* was never employed in attaching and pulling, and in the first lessons it was almost impossible to compel it to take this role. But at the end it spontaneously took this role before any of the other rays, and played the main part in the turning. It is interesting to observe that the ray *e*, which was at first the ray most strongly inclined to play this part, still retains this tendency; the turning is accomplished by the coöperation of this originally active ray, with the one that has been made active by training.

It is evident, however, that we have not yet succeeded in our original undertaking, which was to cause the rays *b* and *c* to coöperate in the turning. Our training thus far has been directed mainly toward *b* alone; it is now necessary to work on the two together.

First, however, it was decided to test whether the effects of the training thus far given would last. The starfish was left for two days undisturbed, then it was given ten trials in succession at three minute intervals. The result showed that the effect of the training had been lost. The ray *e* was used 8 times; *d*, 7 times; *a*, 3 times; *c*, once and *b* only once.

Now, on July 24, a long series of lessons was begun, ten every day at three minute intervals. In these experiments the starfish was so far as possible driven to turn on *b* and *c*, by preventing *a*, *d* and *e* from attaching themselves, or by pulling the latter away if they became attached.

In the first lessons there was again much difficulty in getting *b* to play the active role; in several experiments it absolutely refused, so that *c* was forced to turn the animal unaided. But after four lessons, *b* began to take hold more readily.

Now there appeared again the difficulty caused by the uncoördinated twisting of the tips of *b* and *c*, these usually facing in opposite directions. It was frequently necessary to release one or both of these rays after they had become attached, and to turn the starfish into such a position that the proper side of the ray first touched the bottom. By holding the animal in this position for a time, the tube feet were induced to come out and attach themselves on the proper side. Thus by a tedious process the two rays were induced to take hold in a coördinated way, and to turn the starfish neatly.

At the end of the first ten lessons of this new series, *b* and *c* had acquired a fairly ready inclination to attach themselves, though not in a coördinated way. But if permitted, the other rays attached themselves later, so that the righting reaction became slow, complicated and comparatively ineffective. The starfish was in a transitional stage, when neither the old nor the new way was neatly used, but the two interfered somewhat.

On July 25, *b* and *c* still took hold readily, though usually in an uncoördinated way. The rays just mentioned usually attached themselves first; then other rays took hold if permitted, confusing the reaction. The ray *e* was still bound to play its original part, interfering with the turning inaugurated by *b* and *c*.

On the third day (July 26), the starfish as soon as it was placed on its back took hold with *b* and *c*. But as it was left free, the ray *a* also took hold; *c* was released, and the starfish turned on *a* and *b*. There was still much awkwardness in turning on *b* and *c;* the ten lessons of this day were devoted to practice in this.

The same difficulty appeared on the fourth day, July 27. The rays *b* and *c* took hold readily, but in an uncoördinated way. Much time was spent by the experimenter in inducing them to take hold properly, releasing the wrongly attached rays, turning them into proper position, etc.

This difficulty, due to the uncoördinated turning of *b* and *c*, was never fully met. There would appear to be some permanent peculiarity, perhaps of a structural character, which makes it difficult for *b* and *c* to twist and pull in a coördinated way. The rays *a* and *b* worked together readily, as do also *c* and *d*. The difficulty which *b* and *c* have in working together results in obscuring the effects of training in other respects. The starfish soon came to begin its reaction by attaching *b* and *c* first. But these being placed in an uncoördinated way, other rays were subsequently attached; then either *b* or *c* or both were released, and the turning took place finally on other rays. In a record of the method of final turning therefore, there would be no indication of the effects of training, though this was clearly present in the first action.

The training was thus continued for eighteen days, ten lessons being given per day. The purpose was to determine whether habits of some permanence could be formed,—the former experiments having shown the possibility of temporary modification through training.

At the end of these 18 days (180 lessons), the starfish was allowed to remain undisturbed in the aquarium for twenty-four hours, then was given ten trials without any outside interference. The effects of training showed themselves, as did also the effects of the original tendency. The starfish turned three times out of ten on the rays *b* and *c*. At the beginning, as will be recalled, it never used this pair, and could not be induced to do so even when no other rays were permitted to attach themselves. The results of the ten trials were: $d + e$, 5; $b + c$, 3; $d + c$, 2.

On the following day (after 48 hours without training), ten additional free tests were made, with the following results: $b + c$, 4; $c + d$, 3; $a + e$, 2; $d + e$, 1. Here the effect of training is shown more strongly, the pair $b + c$ being used more often than any other.

Now the starfish was allowed to remain undisturbed for five days. During this time it did not perform the righting reaction at all, and it had had no training for seven days. Ten free trials were then given. The results showed that the habit had disintegrated considerably, but the effects of training were still evident. The righting was rather irregular, two adjacent rays not being used in most cases. The rays were used as follows: e, 5 times; c, 5 times; b, 4 times; d, 4 times, a, 2 times. The pair $b + c$ was used once in combination. Contrast these results with the thirty trials given before training; b is now employed in six times greater proportion, c in three times greater proportion.

Thus it is evident that in the starfish A the effects of training are very marked. Selecting for training a method of turning which the individual never used naturally, and which indeed it at first obstinately refused to employ, we find that immediately after a series of 18 lessons, the starfish used this method spontaneously five times in succession. After a longer course of training, the effects are still very marked, after the lapse of 48 hours, and decidedly evident after a week.

Starfish B.—In the second specimen employed the results were similar to those described under A, so that the details will not be given. The general results, and certain points of special interest will be set forth.

B showed at first a strong tendency to use the ray $a + e$. The result of 25 preliminary experiments gave for adjacent rays the following figures: $a + e$, 15; $a + b$, 3 (p. 143). The pairs $b + c$, $c + d$, and $d + e$ were never used. The ray c was employed less often than any other, being used but three times in 25 trials. As soon as the starfish was inverted, this ray c immediately began to rise and swing over.

It was determined to attempt to train the animal to turn by attaching with the rays c and d and swinging the body over by their aid,—a method never used naturally.

There was at first the same difficulty in getting the starfish B to use *a* and *d* that was found inducing the starfish A to use *b* and *c*. In B, it was the ray *c* that was particularly obstinate. In time this was overcome, and the rays *c* and *d* took hold readily. But their tips usually turned both in the *same direction,* making the turning very difficult. The experimenter was therefore compelled to spend much time in drilling the animal to place these rays properly. For about a week the results of this were discouraging, but at the end of about that period, the effects of the training showed clearly, and the starfish when turned on its back usually at once took hold with *c* and *d* in a coördinated way, and turned itself neatly. Now it was often unnecessary in the course of the lessons to interfere with the animal at all; it at once turned in the way desired. However, for the present I kept close watch and interfered as soon as any other ray showed an inclination to meddle in the matter.

After seven days of training, I determined to test the results. The starfish was allowed to go twenty-four hours without lessons or experiments of any sort. It was then given ten trials, being permitted to turn freely, without interference.

In these ten trials it turned neatly *five times* on *c* and *d,* while the next highest number for any pair was *two,* for *a* and *b*. This result appears remarkable in view of the fact that the combination $c + d$ was never used at the beginning; and it becomes especially striking when we recall what a struggle was required for several days to make *c* and *d* work together at all.

Now ten lessons a day were given for another week. Then after forty-eight hours ten free trials were given. The starfish turned five times out of the ten on $c + d$.

The starfish was now allowed to rest 5 days, so that it had gone seven days without training. Then, on the morning of August 16, it was given ten trials, turning four times on $c + d$. The effects of the training were thus still very evident.

On the afternoon of this same day 15 more trials were given, and now the results of training did not appear so plainly. The combination $c + d$ was used only once, while $d + e$ and $a + b$ were each employed five times. In the entire 25 trials given on this day, the different rays were employed as follows:

a, 11; *b*, 11; *c*, 9; *d*, 11; *e*, 7. The combination $c + d$ was used five times; $a + b$, eight times; $d + e$, six times; $a + e$, once.

Comparing these results with those of the twenty-five experiments before training began, the results of training are still evident. At first, as we have seen, the pair $c + d$ was not used at all, and the starfish could not be induced to employ it. Now it is used in 16% of the cases.

The immediate effects of a brief period of training were tested in a considerable number of individuals, by giving them ten lessons on one or two days, then observing the effects when they were allowed to right themselves freely. In almost all cases the animals when tested immediately after one or two such periods of lessons, continued to turn spontaneously on the rays which they had been trained to use. The effects of so short a period of training did not last for twenty-four hours, however.

In the few cases in which little or no effect of training was apparent, the starfish were large, stiff specimens, evidently older than most of those employed. It seems clear that the behavior of young specimens is more readily modifiable than that of old ones.

After the series of experiments with the starfish A and B were about half finished, and it was clear that success in producing more or less lasting modifications was assured, I began work with three other specimens, F, G and H. The work with these three was done in a more summary way than with the first two, less time being devoted to details and to tests of progress, and the course of training was much shorter. As a result, the training was not so entirely successful in all of these cases. I will give a brief summary of results for each specimen. The rays used by these three starfish in the ten preliminary free reactions are given on page 144.

Starfish F.—Ray *b* never used in the ten free reactions; ray *a* but three times. Training directed toward getting the starfish to turn by the use of $a + b$ for attaching and pulling.

On the first day twelve lessons were given in rapid succession, with but about a minute's interval, the starfish being driven to turn on *a* and *b* by preventing other rays from getting hold. The ray *b* invariably turned so as to face away from *a*, making

the turning very awkward. Nevertheless, at the end of the 12 lessons the starfish had gotten into the way of turning on these two rays. It was now given eight free tests; it turned every time on *a* and *b*, the turning being in each case awkward.

Thus the starfish F readily modified its behavior for a short period, forming what we might call a temporary habit. But owing evidently to the tendency of *b* to place itself wrongly, it was not possible to get the animal to form a lasting habit. After a period of 24 hours, it might first attach itself by *a* and *b*, but finding its position awkward, it attached other rays, released *a* or *b* or both, and turned on the other rays. Thereafter these other rays were given the preference.

I devoted much time to trying to train *b* to twist correctly, by turning it forcibly, by releasing it when wrongly placed and placing it in a new position, etc. But the chief effect of this was to cause, as might perhaps be expected, an apparent reluctance to use the ray *b* at all; the partial habit already formed was broken up by thus hectoring the ray *b* after it had attached itself.

Thus at the end of one week's training, the starfish showed, after the lapse of 24 hours, very little effect of the practice. However, a certain effect appeared, in that the ray *b* was now used almost as frequently as any other—four times out of ten—though at the beginning it had not been used at all.

After another week of training, there was no further improvement, the rays *a* and *b* being merely used with average frequency.

In starfish F, therefore, a temporary habit was readily formed, but a strongly marked lasting habit did not appear under the conditions of experimentation.

Starfish G. Ten preliminary free reactions showed that the starfish used the ray *c*, 8 times; *a*, 4 times; *b*, 3 times; *d*, 3 times; *e*, 2 times. The training was then directed toward getting the starfish to use the ray *c* in a greater proportion of the reactions, —any combination of other rays with *c* being permitted.

After 11 lessons, in which the starfish was compelled to use *c* in various combinations with other rays, the animal was allowed (without an interval of waiting) to right itself 8 times without

interference. It used the ray *c seven* times out of the eight. The temporary habit was thus quickly formed. Similar results were reached on several different days, when the free tests were given in immediate succession to the "lessons".

After one week of training (ten lessons per day) the animal was allowed to rest 24 hours, then was given ten free tests. There was no evidence of the effects of training, the rays being used as follows: *c*, 7; *d*, 4; *b*, 4; *e*, 3; *a*, 2.

During the next seven days, the starfish was given fifteen lessons per day,—five lessons in the morning, five at midday, five in the evening. In these lessons the plan of training was made a little more definite, the starfish being compelled to use the rays *b* and *c* in each reaction. At the end of seven days there was an interval of 24 hours without training. Then ten free experiments gave the following results:

b, 6; *c*, 6; *e*, 4; *d*, 3; *a*, 2.

Thus the effects of the training were very marked after the interval of 24 hours.

Starfish H. This starfish was very large and stiff,—evidently much older than the others. Ten preliminary experiments showed a marked tendency to use the combination $a + c$ (five times) while $b + c$ was, as usual, rarely used (once). The training was directed toward getting the animal to use $b + c$. The method of training differed from that used in other cases. The starfish was placed on its back in a tilted position, and so held for a time, that only the rays *b* and *c* were in contact with the bottom. These rays then attached themselves. The starfish was now allowed to sink flat on its back. Other rays now attempted to take hold, but this was prevented.

Training was in this case quite unsuccessful. It appeared to be extremely difficult for this starfish to turn on the rays *b* and *c*. The ray *b* was invariably twisted in the wrong direction, so that even if *b* and *c* were first attached, the animal later took hold and turned with other rays, if possible. It practically never turned on the rays *b* and *c*, save under duress, and even then only after an obstinate struggle, and in a most awkward way. A week's training, ten lessons a day, had no effect in changing the reaction to *b* and *c*.

The contrast between the stiffness and obstinacy of this large old starfish, and the ready pliability and modifiability of the smaller and younger ones was most noticeable throughout the experiments. It is probably mainly to this that the lack of success with H is due.

The experiments described above establish clearly the ready formation of temporary habits, and the slower formation of habits lasting at least a week. While these experiments represent a very large amount of tedious work, they are of course very incomplete and represent only a preliminary, orienting study of the matter of habit formation in the starfish. It would now be possible with the methods and results thus far worked out as a basis, to make a systematic study of the factors on which habit formation depends; to develop, as it were, a system of educational methods for the starfish. By beginning with young specimens, it is probable that striking results would be reached. Such an investigation would require steady application to extremely dull and tedious work, for a long period.

Two or three special points may be spoken of briefly, rather as general impressions from my experience, than as deductions from precise and extensive data.

The formation of the habit shows itself, as is clear from the account given above, simply in a greater tendency to employ a certain ray or a certain pair of rays in the reaction, not in taking on an absolutely fixed and invariable way of reacting. Consideration of all the facts shows clearly why this should do so. The direction of the righting impulse is determinable by many factors, of which habit is but one. Often other factors work against the habit factor. For example, the direction of the light may tend to cause the animal to turn toward the right, the habit toward the left. Sometimes one factor prevails, sometimes another. The tendency given by the direction of the light rays will sometimes be reinforced by the rays at the right being accidentally the first to come in contact with the bottom; then these two factors together are likely to overcome the tendency due to the habit. When the many factors mentioned on pages 135 to 142 are taken into consideration, it is evident that we can not expect a fixed and invariable habit to be formed,—certainly not without

powerful and long continued action of the habit-forming agent

The same considerations show why a habit once formed is bound to disintegrate when the starfish is left to itself. Suppose that the habit tends to make the animal turn on *a—b*. A combination of other factors may induce it to turn in a given case on *d—e*. As soon as this happens we of course get the beginning of the formation of a new habit,—a tendency to turn on *d—e*. Every lapse from the habit weakens it and tends to start a new one, and the effective factors are so numerous that such lapses must frequently occur. It is quite possible, indeed, that tendencies due to other activities may form or disintegrate special habits in the righting reaction. Thus, if the starfish acquires in any way a tendency to creep with a certain pair of rays in advance it is quite possible that this same pair of rays will tend to play the active part in the righting reaction. Such possibilities deserve a careful study in a systematic investigation of habit-formation in the starfish.

The many factors which may determine the righting reaction will evidently have no constant tendency to make the starfish turn on one given pair of rays; on the contrary, they must sometimes act in one direction, sometimes in another. It is evident, therefore, that we can hardly expect any very fixed habits to be formed, under natural conditions. As we have seen, there is usually some tendency in a given individual to use certain rays somewhat more frequently than others; this is as marked a habit as could be anticipated.

THE UNIFIED IMPULSE AND THE DETERMINATION OF THE VARIED ACTIVITIES UNDER ITS INFLUENCE.

We have thus far dealt with the determination of the action of different parts of the body before the impulse is formed, and with the determination of the direction of the impulse; we have also, in the study of habit-formation, watched the development of the unified impulse. We shall now deal with some general questions presented by the existence of the unified impulse, and particularly with the way in which the action of different parts of the body is determined after the impulse has appeared.

The Problem.—After the impulse to turn in a certain way has appeared, some of the rays bend down, twist, attach themselves and pull; others release, straighten, lift up and swing over; some walk in one direction, some in another,—all co-operating to produce the righting. Our present question is: What determines each of these actions?

This is an entirely different question from that which asks of the factors determining the action of the different parts before the impulse is formed, and a much more difficult one. Before the impulse is formed we can usually give some definite external stimulus or internal relation as the determining factor in the behavior of a given ray or other part; after the impulse appears this can not readily be done. The external stimulus that produces a certain reaction before the impulse is set has no such effect after the impulse appears. Thus, before the impulse, light coming from one side causes the rays of that side to lift, of the other side to bend down and take hold; after the impulse has appeared, the direction of the light has no effect. Before the impulse, contact of the dorsal side of a ray with the bottom causes that ray to twist, attach itself, and pull. After the impulse appears, this twisting and attaching occurs only in those rays that have in some way been predetermined for this role, and they endeavor to perform the action whether they come in contact or not. The other rays do not respond to this contact stimulus at all, or they respond by lifting themselves from the contact. Before the impulse, detaching certain rays causes neighboring rays to attach themselves; after the impulse, the detached rays merely try insistently to re-attach themselves, while the other rays persist in trying to swing over freely. We could take almost every factor mentioned in our list given on pages 135-142, and show that after the impulse is formed its effect is either lost, or becomes entirely different from what it was before the impulse. As we have seen, before the impulse a certain configuration of external conditions may determine a certain method of righting; after the impulse this configuration may be completely changed, or its directive action quite reversed, yet there is no effect on the method of righting. The action becomes, as soon as the impulse appears, to a considerable degree independent of external conditions; it is

largely determined internally, so that what each part of the starfish does may be said in brief to depend mainly on the direction of the impulse.

Effect of External Conditions.—Yet the external conditions of course do affect the course of the action to a certain degree. A certain ray, for example, feels about in the water till it comes in contact with the bottom; thereupon it takes hold and now begins to pull; if it did not come in contact with an external object it of course would not thus change its action. But under the unified impulse there is this peculiarity in the reaction to external conditions: each part reacts to the given external stimulus in such a way as to assist in the righting. One ray, therefore, reacts to contact by holding and pulling, another by releasing, another by walking, etc., as the progress of the reaction requires. It is therefore evident that the external stimulus is not the essential determining factor in these actions. How then are they determined, and wherein consists the unity of the action?

Action of Parts in the Interest of the Whole.—A tempting suggestion comes to the mind, one which if correct might at least lead to a simplified formulation of the unity of action, with a consequent simplification of the problem which it presents. This suggestion is, that every part of the starfish performs that movement which most directly restores it (*i.e.*, this part) to its normal position, with ventral side down. Every movement performed by a given ray, for example, would tend directly to restore the normal position of that ray, and a given ray would perform no movement that tends to oppose this regaining of its normal position. If this statement were correct we should at least be able to account for the movements of each part mainly by the present condition of this part, as determined by its own direct relation to the environment. We should be able to avoid such statements as that one part acts in the interest, not of itself, but of other parts, or of the organism as a whole; or that there is a sort of worked-out *plan* in the behavior, requiring the subordination of certain parts to others. The reaction would still be in many respects difficult to understand, but much less so than in case this suggestion turns out a mistaken one.

The view suggested above could perhaps be maintained for

the righting reaction of the Planarian, as described by Pearl (1903). But the starfish is a much more complex animal than the flatworm, and its righting reaction is much less simply brought about. Careful examination of the facts show that the above suggestion does not hold for the starfish. Certain rays or parts of rays are frequently compelled, in order to facilitate the general result, to move in ways that do not tend to restore their own natural position, or that may indeed have the opposite effect. In the complicated actions by which the righting is brought about there are many that have no direct tendency to restore the part that is acting to the usual position. Thus, when the starfish attaches itself by four of the rays, as in fig. 16, there is usually a complicated "walking" process before the natural position is regained. The two anterior rays (those on the side toward which the animal is turning) begin to walk backward, while the two posterior ones begin to walk forward. Soon the two meet, whereupon the posterior rays release a sufficient number of their suckers so that they can curve upward while still retaining their hold at the tips; they thus permit the anterior rays to walk beneath them, and they re-attach themselves progressively anew as the action is completed. This remarkable walking in opposite directions by the two sets of rays is necessary for the final regaining of the normal position, but does not tend directly to restore these rays themselves to that position.

Often, indeed, a given ray that has partly regained its normal position is compelled, in the interest of the reaction as a whole, to undo what it has already accomplished, to replace itself in the abnormal position after it has gained the normal one. Thus, often certain rays, as *b* and *c*, will have twisted and attached themselves so that the ventral surfaces are down (normal position). Now, certain other rays, as *a* and *e*, likewise attach themselves, and an impulse to turn toward *a*—*e* appears. Thereupon the rays *b*—*c* release and untwist, taking anew the abnormal position; then bend over toward *a*—*e*, till the normal position is restored in a new way. Again, when the starfish turns on three contiguous attached rays (as *a*, *c*, *d*), the middle one of these rays often at first doubles directly back from the tip (not twisting to right or left) so as to get its ventral side down for a considerable portion

of its length. Now, as the other two rays *a* and *d* swing the starfish over in the usual somersault this middle ray *c* straightens out again, thus bringing the entire ray into the abnormal position again, with its entire dorsal side down. The ray now begins to turn again, beginning at the base instead of at the tip. Such reversals, in the interest of the general result, of positions already reached are very common in the righting reaction.

Restatement of the Problem.—Thus it is clear that the behavior under the righting impulse tends toward the accomplishment of a general turning of the starfish as a whole, and that given parts sacrifice their own more direct turning, or even reverse it, in the interest of the general result. The behavior shows what can be hardly characterized otherwise as a general "plan," each part doing what will assist (often very indirectly) to bring about the result. Now, the essential question is: How is it decided what role each part shall play, how decided that it shall play the "*right*" role for bringing about the result? The question could be put in a popular form by using the subjective manner of expression, and saying: "How does each part 'know' which is the proper role for it to play?"[13] Certainly the action is like that of a higher animal when we judge that it "knows" what it is trying to accomplish; "knows" the relation of means to end, and acts accordingly. For characterizing the objective phenomena is such behavior Driesch (1903) coined the expression, "objective knowing" ("Objektalwissen"). The nature of the facts on which Driesch based this term is well illustrated in the righting reaction of the starfish, whatever may be held as to the value of the term or of the further conclusions drawn by Driesch.

Our objective analysis of the behavior has shown us (in agreement with the contention of Driesch) that we can not assign single specific external stimuli as the determining factors for each separate movement. Yet in some way, of course, it is the relation of the organism to the environment that has set in operation the unified action, of which the separate movements are parts, and

[13] The question is given its point by the fact that the role played by each part is not stereotyped, but, speaking generally, any one of many parts may play any one of many roles,—but always playing it in such coordination with the rest as tends to bring about the result.

the course of action is throughout modified by the situation as a whole. The organisms as a unit react to the entire situation, not separately to the separate parts of it. Driesch has expressed this by saying that the entire complex of stimuli has coalesced to form an "individualized stimulus," and that the organism reacts to this individualized stimulus. This statement is doubtless true, but what does it mean as regards the physiological processes that occur? It does not answer the question: What determines at the present moment the present action of any given part? Why does ray *a* now release and rise, while *d* attaches and pulls, etc.?

Driesch's Doctrine of the Entelechy.—We may search for the answer to these questions in two different directions. One is illustrated by the discussion given by Driesch. This leads to the view, partly set forth in Driesch's work on the "Die Seele" (1903), and more fully in a more recent work (1904). This view may be expressed briefly as follows: There is something that may be called a "Psychoid," or, more generally, an "Entelechy," that is interpolated in the chain of action ("mitten in das Geschehen hineingestellt"). This Entelechy is something that intervenes in the action, either by compensating differences in potential between various opposing forces or by putting an end to existing compensation, so that something happens where it otherwise would not, or fails to happen where it otherwise would.[14] This interference of the Entelechy occurs when the interest of the organism requires it, and its action tends to the production of a definite future result.[15] This Entelechy is not a form of energy, nor is it a resultant of the chemico-physical factors present, but is something new and different from the latter.[16] While it is

[14] "Wir wissen über die Einzeläusserung der Entelechie nichts zur Zeit, aber so viel eben kann Allgemein ausgesprochen werden, dass eine "Kompensation," d. h. eine Ausgleichshemmung bestehender Potenzial-differenzen chemisch-aggregativer Art zum Wesentlichsten ihrer Einzelleistungen gehören muss. Hört solche Hemmung auf, so geschieht eben etwas, und sie hört dann auf wenn die Eigenart des Entelechie es infolge von Störungen mit sich bringt." (Driesch, 1904).

[15] Das vitale Agens gibt seine Hemmungen typisch-spezifisch auf, wenn bei normaler Entwicklung oder nach Störungen oder bei Handlungen Typisch-Spezifisches erreicht werden soll." (l. c., p. 185.)

[16] "Ich halte es sehr verbreiteten Denkgewohnheiten gegenüber, für durchaus unzulässig, sich die Entelechie gleichsam als Resultante, wenn auch prinzipiell neuer Art, vorzustellen, welche durch ein zusammenwirken vieler anorganischen Faktoren gleichsam erstünde." (*l. c.*, p. 195.) "Als etwas neues kommt Entelechie zu allen anorganischen Konstanten hinzu." (*l. c.*, p. 203.) "Weiter lässt sich über die Bedingungen des Aufhörens der Hemmung darum nichts sagen, weil die intensive Mannigfaltigkeit der Entelechie etwas Letztes, Naturgegebenes." (*l. c.*)

complex and manifold, it is unanalyzable, final. It is to this Entelechy that the unified action in the interest of the organism is due.

A Physiological Formulation.—A second direction of inquiry leads to the formulation of the processes without leaving the ground of the objective physiological factors which experimental analysis shows to exist, attempting to see how these work together to produce the observed result. An explanation along this line is certain to be incomplete at the present time, or perhaps at any given time,—yet it tends to become more and more complete and satisfactory with the progress of investigation, and this is its great advantage over such an account as that given by Driesch.[17] Such a formulation, making use of the pertinent experimentally determined facts, would take some such form as the following:

The action of any part of the body is determined by the physiological condition of that part at the time the action takes place. The physiological condition of any part is shown by analysis of the facts to be determined by (1) present external stimuli (including under this all the relations of the body to external things); (2) the present relations of the parts of the body to each other (what might be called internal stimuli); (3) past stimuli, external and internal; (4) past actions of the animal; (5) internal chemical changes in the course of metabolism.[18] It is important, further, to recall the fact that the *localization* of stimuli, past and present, is of the greatest importance in determining the movements,—different parts moving differently according as their relation to the region stimulated differs.

Now, in the starfish the following are the facts:

1. The inverted position, with ventral surface not in contact, throws the entire body into a physiological state in which the varied "feeling" movements of the rays and tube-feet occur. The precise movements of each part and the variations in the different parts are determined by the present physiological condition of each part,—this being largely the result of past move-

[17] It is difficult to see how the transferring of the difficulties to an Entelechy that is manifold, yet final, can appeal to anyone as helping us to understand them.

[18] See the summary of the determinants of action in my *Behavior of the Lower Organisms*, pp. 283-292.

ments of that part. Thus, movement in a certain direction induces a state which leads to movement in another direction, etc.[19]

2. While in this physiological state a localized stimulus acts on the body. This may be any of the stimuli enumerated in pages 135-142: light coming from a certain direction, the touching of certain rays to the underlying surface, etc., etc. This localized stimulus is transmitted (evidently mainly by the nervous system) to all parts of the body; it produces a differential effect on the different parts, depending on their position with reference to it. The rays on one side are caused to twist, to send forth tube feet in a certain direction, to attach, and to pull. Those of the other side react differently, releasing, rising up and swinging over, etc., while the intermediate rays are caused to act in a still different way. The different effects produced in different parts depend (1) on the past stimuli and reactions that have affected these parts, and (2) on the localization of these parts with respect to the source of stimulation.

3. But, as we have seen, before the reaction has become well started the localized stimulus may be removed, or it may be localized in an entirely different way, yet the complex reaction continues as before. This shows that the stimulus sets in progress certain processes in the different parts of the body (depending on its localization relative to each part), and that these processes, once started, are not readily stopped; they continue even in spite of the incidence of new stimuli, which would have started a new set of processes if these had not been in progress.

4. Throughout the progress of the differential reaction of the different parts new intercurrent stimuli acting on the various parts causes them to modify slightly their method of behavior without altering the general trend of the processes of turning; the tube-feet attach when they come in contact, etc., etc., so that there is throughout an adaptation to the present conditions.

5. As soon as the normal position is restored this restores again the normal physiological condition that existed before the inversion of the animal; as a result all the processes involved in the reaction cease.

[19] Compare the account of these relations in the earthworm (Jennings, 1906 *a*).

It is evident that the difficult point in this formulation comes in the second paragraph above. Why should the stimulus, localized in a certain way, cause not merely different reactions in different parts (which is not in itself remarkable), but precisely those different reactions which will work harmoniously together to accomplish the result of righting the starfish?

Two Possible Answers.—To this two answers are possible. (1) The first is that which follows from Driesch's formulation; the harmonious, purposive action is due to the Entelechy. (2) The only other answer that can be given is that the precise way each part shall act under the influence of the stimulus must be determined by the past history of that part; by the stimuli that have acted upon it, by the reactions which it has given, by the results which these reactions have produced[20] (as well as by the present relations of this part to other parts, and by the immediate effects of its present action). In other words, this complex harmonious working of the parts together is only intelligible on the view that there is a history behind it; that it is a result of development. We can not look upon it as a final thing ("etwas Letztes, Naturgegebenes"), because there *is* a history behind it, and we know as solidly as we know anything in physiology that the history of an organism does modify it and its actions—in ways not yet thoroughly understood, doubtless, yet none the less real. The starfish that we have before us has an actual history of untold ages, in which it has existed as germ plasm or otherwise, and there can be no greater mistake in physiology than to leave this out of account. The modifications induced in organisms by their experiences, either while existing as germ plasms or as individuals, are as clearly a part of physiology as is the study of digestion, and their existence is not less doubtful.

Development of the Unity of Action.—Have we any evidence that the harmonious working together of the different parts under the action of the righting impulse *is* the result of a development? Clearly, we have; our experiments on habit formation show that individual experience plays a marked part in the reaction. We see that when an animal having a set impulse is

[20] All these factors have been *demonstrated* to so modify organs or organisms as to change their behavior in definite ways.

prevented from righting itself in accordance with this impulse there does not appear at once a completely harmonious new impulse. On the contrary, the starfish for a long time rights itself in awkward ways, certain rays playing a part (as a result of their former history) that tends to impede rather than assist the progress of the reaction; such, for example, is the action of the ray *e* in the history of the starfish *A* (p. 161).

Imperfect Unity.—The fact that there are thus at times, in the process of righting, certain actions that do not lead toward the general result, but actually impede it, is worthy of thought. In many cases the accuracy and harmony of the righting impulse is striking, as we have set forth above. But the existence of imperfect impulses, with certain of the actions uncoördinated, is certainly significant. It will be well to cite certain cases from my notes.

Thus, in the preliminary experiments to determine the usual method of righting in the starfish *B*, I noted that "there is a pronounced tendency for *a*—*c* to do the main part of the work," and that "*d* commonly gets hold and pulls also, but really delays operations considerably." The turning would have taken place much more neatly and quickly if *d* had refrained from interfering. Again, in testing the starfish *C*, I noted that "*d* gets hold, begins to turn the starfish, unaided, toward the ray *e*; now the ray *e* gets hold on the other side and delays the process." In many cases, where it is necessary for certain rays to detach themselves in order that the turning may take place, they continue for a considerable time to hold, complicating and delaying the process. At times the impulse appears quite unified and harmonious, save that a single ray appears to be excluded from it; this ray holds with its suckers and resists the action of the other rays. In a few cases I have seen such a ray actually pulled by main force from its attachment by the activity of the other rays.

Thus at times the impulse is not a perfect thing; the action is discordant. I do not mean to represent this as the usual case, for it is not, but the existence of these inharmonious activities must be remembered in forming a theory of the matter. It would appear to be difficult to account for these cases on the view that an entelechy controls the movement in the interest of the organism.

After we have assumed the existence of a non-physico-chemical entity whose essence it is to control the physico-chemical process in the way required to bring about harmonious, "specific and typical" action, it is difficult to see why the processes should sometimes not progress harmoniously, or why all should be in harmony but certain ones. On the other hand, if we hold that this harmony is a secondary result of the operation of many factors whose co-operation is the result of a development, then this occasional imperfection is just what we should expect.

While the experiments on habit formation show that the harmonious impulse is subject to development in the history of the individual, I would, of course, not by any means maintain that this accounts in full for the unity of the impulse. There is, in addition, the history of the "germ plasm" to be considered: much has come to the individual through heredity. How these hereditary properties have been acquired we do not know; here is a problem for analytical experimentation for coming generations of investigators.

Imperfect Solution of the Problem on Purely Physiological Grounds.—The physiological formulation then leaves the problem in this condition: (1) The impulse is not always perfect and concordant, indicating that it is not the reflection of a perfect and concordant entity, but is a product of development; (2) the development of the harmonious impulse can be traced partly to individual history, in the process of habit-formation, and many of the factors on which it depends can be set forth, though this does not account for the whole; (3) in addition to the individual development, there is racial development, whose laws we have as yet made little progress in tracing. The unsolved part of the problem (confessedly a large part) lies in this field of the laws of racial development; a solution will not come until these laws are worked out.

The Entelechy Doctrine a Renunciation of all Solution.—It is to meet the difficulty for which we have appealed to the study of the laws of racial development that Driesch assumes the existence of the Entelechy. It is probable that investigators would be as ready to accept the entelechy doctrine as any other scientific explanation, provided that they could see that it *is* an explanation.

There are certainly enough dark places in biology to make any doctrine welcome that can clear them up. But to many it appears that to assume the existence of an entelechy of the sort that Driesch sets forth does not help in our understanding of matters in the least. It seems to be merely a way of collecting all the difficulties together and giving the bundle a name. The difficulties continue to exist as before. Thus, suppose that we attribute the co-ordination of action of all parts of the starfish in the righting impulse to an Entelechy. Then we still have the question: How does there happen to be in the starfish this something that can produce precisely the complex harmonious action that we are endeavoring to understand? We have merely transferred the complexity and harmony to this something,—the Entelechy. The question remains: How does the Entelechy get it? Surely if a complex harmonious action leading to a definite end is something requiring analysis and explanation, or implying a development, it is equally so whether it is found in a physico-chemical complex or in an Entelechy! To many investigators the mind that requires analysis and explanation of these things when they are found in an animal or in a physico-chemical complex, but can swallow them whole when presented under the name of an Entelechy, presents a curious contradiction in requirements. To accept the Entelechy unanalyzed and unexplained is merely to give up the problem as insoluble. But if we refuse to admit for the Entelechy what we can not admit for the physico-chemical complex, and are to proceed to a study of the comparative development of entelechies, tracing their origin and accounting for their complexities by development from simpler conditions in accordance with known laws,—then surely we are merely transferring our problem from the complex that we actually find in time and space to a sort of manufactured copy of this problem, presenting the same difficulties, with the additional one that it is impalpable and can not be directly dealt with at all. The entelechy simply adds to our difficulties.

Again, suppose we leave aside all question as to the origin of the complex powers of the Entelechy, merely admitting its existence as something "Letztes, Naturgegebenes," and believing that it determines the harmonious movements of the starfish in right-

ing itself. How does our problem now differ from what we had before? There still remains the question: How is the specific, differential action of each part to be accounted for? We find that these actions have certain complex relations to the localization of certain external stimuli; to the action of certain past stimuli, etc., etc. Admitting that the Entelechy brings about these actions and relations, we must still ask: How does it bring them about? How does it cause ray *a* to act in one way, ray *b* in another, with relation to the localized stimuli, present or past? In attempting to answer these questions we can only have recourse as before to changes in physiological state, to conduction by the nerves, etc., etc., exactly as was done before the Entelechy was brought into the matter at all. In other words, the original problem is still present in its entirety. It is difficult to comprehend how any investigator, accustomed to the experimental and conceptual analysis of complex phenomena, can hold that he has gained any insight into such a matter if he is merely told that the Entelechy determines the various actions.

Why has so acute an investigator and thinker as Driesch set up such a theory as that of the Entelechy? It has certainly not been without grounds of some sort. There are indeed grounds on which the existence of some such entity as the psychoid or Entelechy might be maintained. One might hold that certain phenomena directly indicate the existence of such an entity. Thus, what *is* the unified impulse that we see appearing at a certain moment? It is certainly a natural tendency of the mind to put something behind what we actually see in such a phenomenon; to say that "the starfish decides" at that moment what to do,—thinking of the starfish as an individual. Considering it an individual, one might well hold that there is, as Driesch expresses it, a sort of "constant of individuality," which might be called a psychoid or Entelechy. This view might conceivably be supported by comparison with what we know (by introspection) in man, the starfish being considered to have something corresponding to what we call the "mind" of man. The existence of this entity would be maintained quite independently of the question whether it makes the phenomena more intelligible or not. It seems probable that such considerations have actually aided in the

formation of the doctrine of the Entelechy; possibly they are ultimately the real basis for it. But this kind of Entelechy, far from helping us to understand organic phenomena, would be an additional fact to be explained,—one far more difficult than that which the objective phenomena present. The Entelechy would be a problem, not a solution.

The reason for the lack of general acceptance by men of science of any such doctrine as that of the Entelechy is thus in most cases not on account of an obstinate prejudice in favor of physics and chemistry, but merely because they perceive that the Entelechy does not help in the least in the solution of the problems with which they are confronted. Conversation with investigators leads me to believe that a large proportion of them would welcome a distinctively "vital" explanation as readily as any other, if they could see that it helped them in understanding and controlling the activities of organisms. But such a view as that of Driesch merely transfers the problems to the Entelechy, where they are less attackable than before. To use a most expressive characterization applied by Driesch to the Weismannian theory, it only gives us a *photograph* of the problems. Surely it makes the problems no more intelligible to enclose them in an Entelechy than to do them up in a chromosome!

The Problem One Whose Solution is to be Completed in the Future.—Investigators may hold with Driesch, as the present writer does, that most of the simple chemical and physical explanations that have recently been given are superficial and quite inadequate to account for the regulatory activities of organisms, and may believe that Driesch has done a great service in emphasizing this. But, at the same time, they hold it equally evident that such a doctrine as that of the Entelechy does not help us: such I believe to be the views of a majority of those engaged in research. We are not forced to hold either that the regulatory activities of organisms have been explained by chemistry and physics or that they are brought about by an Entelechy. We can hold, in preference to either of these views, that our present analysis is incomplete, and that there will be something for investigators to work out in these fields during the next ten thousand years or so. Both the rash assertion that we have already

accounted for these things in simple chemical and physical ways, and the hasty recourse to entelechies and the like, seem due only to the impatient demand for an immediate and final explanation at all cost. And the price paid for the explanation by the Entelechy appears to be the giving up of all hope of any real understanding, leaving our descendants for the next few thousand generations cut off from all opportunity to solve any of the fundamental problems by the methods of experiment and analysis.

Concluding Statement.

The foregoing account is intended partly to serve as a storehouse of objective facts, for reference when information concerning the behavior of the starfish is required, in order that there may be no farther excuse for theories that leave out of account the facts. It is therefore not practicable to make a summary that will really represent the results set forth in the paper. To form an idea of the matters treated, reference should be made to the table of contents.

Perhaps the most important thing developed in the paper is the demonstration of the variability, modifiability, unity and adaptiveness in the main features of the behavior of the starfish. The movements are shown to depend on the varying physiological conditions of the animal, and the numerous factors which demonstrably modify the physiological condition, and therefore, the behavior, are set forth in detail. Habit formation is demonstrated and discussed in full. The unity and co-ordination of much of the behavior is presented, and some theories of its nature and origin are discussed. Of subordinate importance are the essentially new, correct accounts of the method of locomotion and of the way in which the negative reactions occur.

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CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XIX

THE EARLY LIFE-HISTORY OF *DOLICHOGLOSSUS PUSILLUS* RITTER

BY

B. M. DAVIS

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ERRATA: On page 214, last line, for *D. kowalevski*, read *B. kowalevskii*.

On page 218, explanation of Plate 4, last line, for × 1, read × 4.

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CONTENTS.

PAGE

Introduction ... 188
Periods of Development ... 190
Early Habits and Activities of *D. pusillus* ... 192
Period I ... 192
Period II ... 192
Period III ... 194
Periods of Development Correlated with Habits and Distribution of Adults ... 195
Early Growth Stages ... 200
External Features. Period I ... 200
Egg ... 200
First to Sixth Cleavages ... 201
Comparison of *D. pusillus* with Amphioxus and with Ascidia (*Ciona intestinalis*) in their Early Cleavage ... 203
Blastula ... 204
Gastrula ... 204
Larva within the Egg-capsule ... 205
Period II ... 205
Period III ... 205
Internal Features. Period I ... 205
Blastula ... 205
Gastrula ... 206
Mesoderm and Body Cavities ... 207
Gland Cells ... 212
Occurrence of Half Embryos and Double Embryos ... 213
Comparison of *D. pusillus* and Amphioxus with reference to Origin of Body Cavities ... 213
Bibliography ... 216

INTRODUCTION.

In November, 1902, I secured a few eggs and free larvae of *D. pusillus* Ritter, a short account of which is given in a recent paper (Ritter-Davis '04). In this account it is stated that owing to destruction of collecting grounds at San Pedro, California, it would be impossible to secure a complete series of stages necessary for detailed study, but that it was hoped to obtain sufficient material at San Diego, California. On January 18, 1905, I had the good fortune to find a small area of mud flats on the west side of Whaler's Bight, San Diego Bay, containing *D. pusillus* at the height of its breeding season. During the month following (January 18 to February 18) I succeeded in getting all stages from unsegmented egg to metamorphosis, and was able to study these stages in the living condition.

The only account we have of direct development of Enteropneusta is that by Bateson '84-'85. This has become one of the zoological classics. However, Bateson's series of early stages was not complete, and he did not give a detailed account of the animal's activities at different periods of its development.

Further investigation of the subject is an urgent desideratum. In this paper I give an account of the habits and activities of the early life of *D. pusillus,* and also the stages of development up to and including that of the formation of the body cavities.

At another time I hope to follow out the later stages of development, particularly of the connective tissue system and supporting framework. I take pleasure in acknowledging the helpful suggestions and directions which I have received in the preparation of this paper from Professor William E. Ritter.

MATERIAL AND METHODS.

The portion of the mud flats on which the animals live is uncovered at mean low tide so that collecting is possible for several hours during five or six days of each low tide period. This fact is important, for the work of collecting is slow and tedious, as a great many burrows must be examined before one is found containing eggs.

D. pusillus has its burrow near the surface, but there are no external indications of its presence except occasionally when the animal extends its proboscis from the burrow (Ritter '02). A certain amount of prospecting is therefore necessary before the animals are found in large numbers.

When such a place is found, a spadeful of mud is dug up and the burrow of each animal carefully examined for eggs. By breaking one side of the burrow and gently lifting the animal out or pushing it aside, the eggs, if present, may be seen clinging to the unbroken side. They are usually closely packed and sometimes extend over an area of several square millimeters. The position of the eggs in a burrow is shown in plate 4. Here the animal has been lifted up and to one side, leaving the eggs exposed. The eggs are somewhat flattened, whereas in water they are perfectly round. They also appear to be of a darker tint of yellow ochre than when seen in water. This is due to the dark background of the mud.

From the burrow the eggs are removed by means of a fine pipette to a shallow dish filled with clear water. By holding the dish against a white background, the eggs may be easily separated from the particles of sand, and then transferred to small vials of sea-water for transportation. As eggs or larvae of a single burrow are usually in nearly the same stage of development, when a large number in one burrow is found, they are kept in a separate vial. On reaching the laboratory the material is transferred from vials to small dishes filled with fresh sea-water. An occasional change of water is all that is necessary to keep the animals alive.

Zenker's fluid, corrosive-acetic mixture, Lo Bianco's chrom-osmic mixture, and osmic acid were used as killing and fixing agents. After fixation and washing the specimens were preserved in eighty per cent. alcohol. Eggs or larvae from single burrows were kept in separate dishes. Some were killed and preserved from time to time, the intervals depending upon stage of development. Fifteen such series were made.

Various stains were used, including Mallory's connective tissue stain, Meyer's acid haemalum, Benda's iron haematoxylin, Heidenhain's iron haematoxylin, Delafield's haematoxylin, and

borax carmine. Congo red, erythrosin, eosin, and orange-G were used as counter stains. Of these Meyer's haemalum counterstained with congo red for the early stages, and Mallory's connective tissue stain for advanced stages that were fixed in Zenker's fluid proved to be the most satisfactory.

Living material was examined with a Zeiss-Greenough stereoscopic microscope. The depth of field and appearance of three dimensions afforded by this instrument added greatly to the accuracy and facility of observations, particularly in the detailed study of swimming.

PERIODS OF DEVELOPMENT.

The following statement made in a previous paper (Ritter-Davis '04, p. 173) in regard to periods of larval life of Tornaria, applies to *D. pusillus:* "In the larval life of the enteropneusta three periods should be recognized; namely, a period of *larval development;* a *climactic* period; and a *metamorphic* period; *i.e.*, a period of development again, but this time development toward the adult animal."

As I shall recognize these periods in my account of the early life history of *D. pusillus*, it will be necessary to modify somewhat the definition previously given, particularly since no account was taken of the earliest developmental stages of tornaria.

The first period, or period of larval development, includes the time passed wholly within the egg-membranes. It may be noted that my observations on the time of hatching do not reveal any such irregularity as described by Bateson for *B. kowalevskii.* After describing that stage of the larva where the collar area is definitely marked off by anterior and posterior grooves, he says: "The animal remains in this condition for some hours and is generally hatched without the occurrence of any further alteration. The time of hatching is, however, quite irregular. Larvae may frequently be found swimming freely whose organization is not much in advance of Stage C (the stage before either groove has appeared), and on the other hand, I have seen them in the condition of Stage G (after appearance of first gill opening) in the eggshell." (Bateson '84, p. 211.)

My observations agree substantially with the first part of this statement, but not with that part referring to irregularity of hatching. In his second paper (Bateson '85, p. 2) he says: "From further observation it seems probable that this period (Stage D) assigned as the time of hatching is too early; for embryos kept in aquaria do not break the membranous shell before Stage G is reached. Probably, therefore, the larvae found swimming in Stage D had escaped owing to an artificial rupture of the shell during the process by which they were found,[1] an account of which is given in an appendix."

I am inclined to think that the presence of late unhatched larvae is also abnormal and exceptional. As will be described in detail later, the stages of normal larvae immediately preceding hatching is one of great activity within the egg-shell. It might be supposed that in exceptional cases larvae would not be sufficiently active to effect an opening. In such cases there is no apparent reason why the larvae should not pass through the later stages of development within the egg-shell; no instance of this kind, however, has come within my observation.

The second or climactic period includes the period of active swimming.

The third or metamorphic period includes two phases: one of rapid crawling, mainly by means of the ciliary band, and one of slow crawling, by means of proboscis and body cilia.

These periods are not absolutely distinct in the sense of being delimited from one another. Period II gradually merges into period III by the active swimming cycles, as will subsequently be described, becoming less frequent. The same is true of the two phases of period III, for the movements by means of proboscis and small cilia are gradually substituted for those made by the ciliary band. The three periods above described will hereafter be referred to by their numbers: I, II, III.

[1] The essential steps of this process are as follows: (*a*) Shake up mud in vessel, avoiding rotary currents; (*b*) put in this, minced balanoglossus and allow to settle a few minutes; (*c*) siphon off lighter particles in suspension until balanoglossus fragments are reached; (*d*) draw this portion off and in it will be found the embryos.

EARLY HABITS AND ACTIVITIES OF *D. pusillus.*

Period I.

As soon as the ciliary band is fully formed, the larva begins active swimming within the egg-capsule. Bateson '84 (p. 211) says: "The larva swims about very rapidly, rubbing the membranous shell with its anterior end until it gives way, and the animal escapes." The larva of *D. pusillus* does not escape as easily as one might suppose from the above statement. As soon as an opening is made, the anterior end is pushed through. The proboscis becomes flattened and the body within the capsule constricted. The large cilia cease to move, but the small ones are in active motion, producing a slow rotation. The crucial point in the process of hatching is in the passage of the ciliary band. After this portion of the body passes through the opening, the larva is soon free. The average time for the entire process after the opening is made, as observed in five specimens, was twenty minutes. Within a few minutes after escape from the egg the larva begins active swimming. Plate 7, figs. 17, *a*, *b*, and *c*, represents the passage of the larva through the egg case opening.

Period II.

As will be noted in connection with the description of period III, period II was not noticed at San Pedro. Bateson '84 (p. 211) says: "On leaving the egg it does not swim at the surface as pelagic larvae do, but creeps about in the mud, burrowing with its proboscis, in the walls of which muscle fibers soon appear, and also propelling itself by means of its ciliated band. If placed in a beaker of water it sinks to the bottom at once." This description, with the exception of one point, applies very well to the third period of *D. pusillus*, but not to the stage immediately following escape from the egg, or period II. The exception above noted is in reference to what Bateson says of "burrowing with its proboscis, in the walls of which muscle fibers soon appear." It is hard to understand how the animal could burrow with its proboscis before the muscle fibers appear and become active. As a matter of fact in *D pusillus* when the burrowing stage is reached two sets of muscle fibers have appeared in the proboscis.

Period II in *D. pusillus* is a time of active swimming, and varies in length from twelve to twenty-four hours as shown in observation of twelve individuals. Intervals of rest occur, during the period, and these become longer as the larva grows older. When swimming actively the larva appears much like a miniature tornaria, both in outline and relative length of longer and shorter axes. However, the similarity goes further than this. Like tornaria it swims chiefly from below upward. It may occasionally take a horizontal course, but this is always undulatory and never in a straight line. Like tornaria, its swimming movements are produced by the cilia of the ciliary band. Like tornaria, also, it does not swim vertically upward but takes a spiral course, the direction of the spiral, as in tornaria, being clockwise.

Unlike tornaria, as far as has been observed, it has a regular cycle of movements which is repeated at rather regular intervals. Beginning at the bottom it swims vertically upward always describing a spiral. When near the surface of the water the direction becomes horizontal and the path undulatory instead of spiral; then the animal ceases to swim and falls rapidly to the bottom. The bottom having been reached, after a short period of rest, the cycle of movements is repeated. Sometimes a new cycle may begin before the bottom is reached.

The following is a tabulation of a typical series of swimming cycles:

Time of rising through distance of 25mm.	Time of horizontal swimming.	Time of falling.	Time of rest at bottom.
40 secs.	15 secs.	10 secs.	No secs.
35 secs.	15 secs.	8 secs.	60 secs.
30 secs.	Half way down and	....	90 secs.
	new cycle begun	20 secs.	1 sec.
30 secs.	105 secs.	14 secs.	No secs.
25 secs.	10 secs.	11 secs.	2 secs.
32 secs.	1 sec.	New cycle half way	
30 secs.	5 secs.	New cycle one-third way down	
	8 secs.	12 secs.	6 secs.
	40 secs.	9 secs.	70 secs.
35 secs.	1 sec.	New cycle two-thirds	
25 secs.	2 secs.	way down	
	3 secs.	8 secs.	1 sec.
32 secs.	1 sec.	9 secs.	40 secs.

After several hours the intervals of rest at the bottom grow longer and longer until finally the animal ceases to rise. Light does not seem to have any influence in directing the animal's movements. It swims freely both toward and away from the light. A number of animals were put in a dish from which light was excluded except at a small opening in the cover of the dish. The dish was left undisturbed for five minutes. At the end of this time the animals were found scattered irregularly through the water. This experiment was modified in various ways, and for varying lengths of time, but always with negative results.

It is during period II that the tuft of apical cilia reaches its fullest development, although it appears in period I. There is reason to suppose that these cilia are of use to the animal at this time. It is impossible to ascertain their exact behavior when the animal is moving rapidly, but when it moves slowly along the bottom of a dish by means of the small cilia with which the body is covered, the tuft swings in a direction opposite that which the animal takes in turning, thus playing the part of a tiller or rudder for steering the creature. It is probable that these large cilia are used in a similar way during the animal's more active movements. But the direction is not determined entirely by the apical cilia, for only one part of the ciliary band may beat at a time; *e.g.*, slow rotation is caused when the cilia of one region on one side beat while the rest are inactive. Furthermore, the rate as well as the direction of swimming is determined by the number of cilia that beat in the ciliary band. The velocity of swimming may be said to vary with the number of cilia in action. When the velocity is increased, as it always is when the animal is rising, this is probably always accomplished by use of additional cilia. In one portion of the swimming cycle the descent is vertical. The cilia of the ciliary band are, at such times, entirely motionless.

Period III.

The few specimens examined at San Pedro in 1902 consisted of unhatched larvae (period I), and free larvae of period III. From the scanty material then at hand I concluded with Bateson that the first period after hatching was a crawling one, and that there was no free swimming period. My observations were de-

scribed in these words: "Animals do not swim freely, but glide about with proboscis pointed forward over the supporting surface. These movements are made mainly by means of the large cilia composing the posterior ciliated band, although their action ceases occasionally for short periods. At such times the animal continues to move by means of minute cilia with which the body is covered, but the motion is very slow." Ritter-Davis '04, pp. 201-202. This is correct for the first phase of period III. As the larva grows older there is less and less use of the ciliary band until finally it is not used at all; at least there is no more rapid creeping.

During the latter part of the first phase of period III, at times when the ciliary band is not in use, considerable muscular activity may be noticed in the proboscis, this member now contracting and extending alternately. These movements are characteristic of the second part of period III. By them, and also through the action of the small body-cilia, the animal is able to creep slowly about over the supporting surface. Bits of sand and other sediment readily adhere to the body in the region of the collar, collected there by the mucus or slime which is actively secreted at this time. The secretion in one instance was so much that two larvae that happened to meet were bound together, and so closely that neither could escape by its own efforts. In older stages the accumulation of sediment was so great as to necessitate its removal before the animals could be studied.

It is at this time that the larva begins to burrow. When placed in a dish of mud it soon disappears beneath the surface. The burrowing movements of *D. pusillus* are very similar to those of the larva described by Morgan '94, p. 17. He says: "It was very noticeable that so soon as the proboscis was thrust in the sand a thick mucus was thrown out from the surface of the proboscis and collar region to which the sand granules stick, forming an irregular tube around the animal."

Periods of development correlated with habits and distribution of adults.

The adult life of *D. pusillus* is passed in burrows in the mud. The animal does not, as many sand-dwelling animals do, come to

the surface and migrate to new areas. It is true that occasionally the proboscis is protruded above ground, but with the rising tide this is again withdrawn. Careful observations have failed to discover any instance where the animal's body is in any way exposed after the ground is covered with water. (Ritter '02, p. 255.)

It is also very probable that any individual animal is restricted to a comparatively small area; that it does not migrate from place to place in the mud. This is indicated by the fact that burrows are vertical for the most part, and that the burrowing movements are slow compared, for example, with those of certain nemertians and annelids. Furthermore, the adult animals are not uniformly distributed over the area in which they are found. In some places as many as fifty individuals may be found in an area of one square foot, while in others but one individual may be found in an area of a square yard.

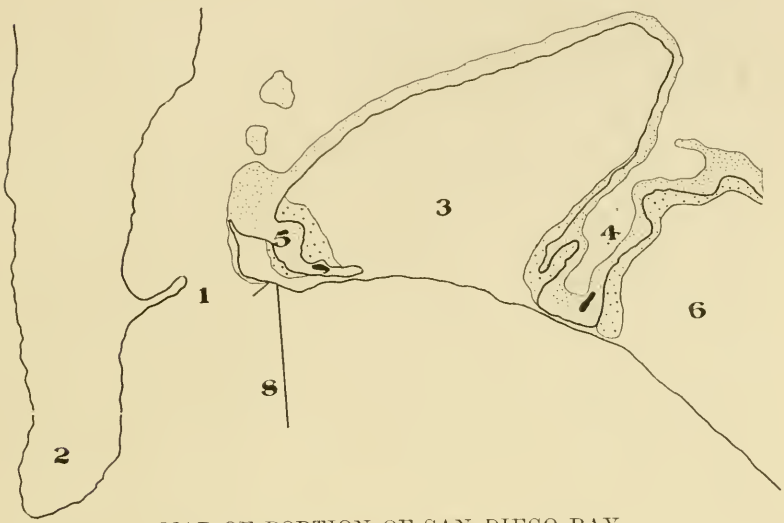
The distribution of *D. pusillus* during a period of six years at San Pedro, California, is described as follows: "The area of greatest numbers has gradually shifted toward the mouth of the harbor. None were found in 1902 in places where they were abundant in 1897. In 1900 there were two areas of distribution, one at low tide-mark, where large individuals predominated; the other considerably above low tide-mark, where small ones predominated." (Ritter-Davis '04, p. 200.)

Here are two points worthy of notice. The shifting must not be understood as migration in the sense of individuals moving toward the mouth of the harbor, but rather as plants migrate. For various reasons, among them being deposition of sediment, change of currents, and invasion of eel-grass, the region populated in 1897 became unfavorable for enteropneust life, and the animals died. The opposite end of the mud-flat strip which was the center of distribution in 1902 became so by the growth of new individuals. In 1900 the increased number of new individuals was great enough to be noticeable but in another direction of distribution. Here they appeared farther shoreward.

Before discussing means of dispersal for *D. pusillus* it will be worth while to consider more in detail the environment of the adult. The animal is always found in sheltered places, free from

swift currents and disturbing waves. It is in such places that fine, black mud, rich in organic matter, occurs. The animal is never found in even moderately clean sand.

The black-mud areas are associated with level surfaces which are uncovered at low tide, with freedom from wave action, and



MAP OF PORTION OF SAN DIEGO BAY.

1. Entrance to San Diego Bay.
2. Point Loma.
3. North Island.
4. Spanish Bight.
5. Whaler's Bight.
6. Coronado.
8. Government breakwater.

Heavy black shading in 4 and 5 indicates area of distribution of *D. pusillus*.

Region indicated by fine dots uncovered at low tide.

Region indicated by large dots covered at high tide.

with marginal plant growth, part of which is submerged at very high tides. Whaler's Bight and Spanish Bight of San Diego Bay are typical illustrations of just such conditions. The map (p. 197) is part of the San Diego Bay including the above bights. A reference to this map will indicate to what extent these conditions obtain in the area of distribution of *D. pusillus*.

I have already stated that such situations are free from swift currents and strong waves. The tidal currents in these extensive flats are unnoticeable on casual observation. With this environment in mind we are ready to consider how the early life-stages of the animal are correlated with these conditions. Period I is spent in the egg-capsule in the security of the burrow. Here all the developmental changes, fitting the animal for the active life of period II, take place, and the beginning is made of the organs of greatest functional importance for period III, *viz.*, muscles and mucus glands.

Although no accurate determinations were made of the specific gravity of the organism, it was obvious from watching individuals of the three periods that this is least during period II, as in tornaria. The important characters of period II which are correlated with the animal's movements are: diminished specific gravity, brought about, no doubt, in part as will be indicated, by the enlargement of the middle and posterior cavities; the climax of efficiency of ciliary activity, in both the ciliary band and apical tuft; and absence of growth, except of muscles and glands, whereby the animal's energy may be more completely used in swimming.

The activities of the organism at this period are directed, first, to escape from the burrow of the parent, and second, to its suspension in the water during short intervals of time. I say "in suspension," for a little calculation shows that it could not proceed by swimming more than two or three meters during this entire period, and when we consider that the direction of swimming is mostly vertical, the actual horizontal progress would be much less.

Obviously, this part of the animal's life is adapted to make use of the slow tidal currents for dispersal. Judging from the numerous laboratory experiments already described, the swimming cycles would prevent the animal from being carried very far into deep water, for the time of rest at the bottom is often greater than the time of active swimming. Besides we must also take into consideration the fact that the tide moves in a direction away from the deep water as well as toward it. The actual procedure from the burrow of the parent is somewhat as

follows: First, a cycle of swimming keeps the animal suspended for a short time, during which it is borne by the tidal current; second, a period of rest on the surface of the mud, until the beginning of the next cycle. This process being repeated for from twelve to twenty-four hours, the animal would, during this time, be carried a considerable distance from the parental burrow, at least far enough to account for such migrations as are described for San Pedro Bay. (Ritter-Davis '04.)

During the latter part of this period the intervals of rest are longer and longer, until by the time period III is reached the creature is safely located in the region of its future burrow.

What induces these swimming cycles is by no means clear. Two possibilities are suggested: one of stimulation, the other of rhythmical physiological states.

In the consideration of stimuli the factor of light must be excluded, since the organism has been shown to be indifferent to light. The only source of stimulation would seem to be contact with the surface of the mud, for temperature, salinity, oxygen content of the water and other conceivable factors are practically constant.

When Paramoecium comes in contact with a solid or other source of stimulation, a new cycle of movements is instituted (Jennings '04). At first thought it might seem that the free-swimming larva of *D. pusillus* behaves in the same way. If, as it touches the mud a new cycle were to begin immediately, the behavior of the two organisms would be essentially the same. But the larva crawls for awhile on the mud, and these crawling periods, even at the height of period II, vary in length. Again, a new cycle is often begun before the animal reaches the mud. This precludes the possibility of contact as a stimulus. It would seem, therefore, impossible to assign any particular stimulus as a cause for starting the swimming cycle.

As to these cycles being rhythmical and due to physiological states, the chief objection is that they are not regular either in point of time or extent of movement. In the behavior of Paramoecium and similar organisms where this explanation seems plausible, the animals are adults, and the physiological conditions are fairly constant. In the animal under present consideration,

the physiological conditions would not be expected to be constant, since they would be interfered with by growth, which, though reduced, is nevertheless going on. But might not the cycles which would otherwise be rhythmical due to one set of physiological conditions be modified by another set, *e.g.,* that of growth, so as to bring about just such irregularity of swimming cycles as is found? The fact that these cycles become more and more irregular toward the end of period II, when internal changes are becoming more active just previous to period III, lends some credence to this explanation, and makes it plausible but by no means certain.

As has already been stated, the first phase of period III is characterized by rapid crawling in which the now motile proboscis begins to take part. This is an adaptation which is important for preservation of the animal at low tide, for it is enabled to burrow in the soft ooze and thus readily escape destruction.

The second phase is really metamorphic. The animal's movements are mainly muscular. The mucous glands are sufficiently numerous and active to pour out abundant secretion for cementing the walls of its burrow and lubricating them with slime.

The yolk supplied by the egg is now nearly used up as indicated by the transparency of the animal (Bateson '84), and by the absence of yolk granules as shown by microscopical examination. But in the meantime a mouth, digestive tract, and gills have appeared, thus equipping the organism for self-support.

EARLY GROWTH STAGES.

External Features.—Period I.

Egg. The method of discharging the ova, and the general characters of the egg itself are adequately described by Ritter-Davis '04. The enteropneust egg has two membranes, a fact hitherto unnoticed. At first, these are so closely adherent to each other as to be indistinguishable, but later they are separated by a narrow space. The outer membrane may then be removed, leaving the inner one intact. This is often necessary in order to study the larva within the capsule when the outer membrane is

rendered partially opaque by accumulation of sediment. While no special observations were made on the nature of these membranes, it was noticed that, just before hatching, the outer one became less transparent and less resistant. The latter condition is correlated with the hatching process which has already been described.

The particular feature of the egg in this stage is its opacity. Bateson's statement that the egg of *D. kowalevskii* is "very opaque" is equally applicable to that of *D. pusillus*. The opacity is due to the yolk granules which are uniformly scattered throughout the cell. This distribution is so uniform that no difference such as described for the ascidian egg by Conklin and by Castle may be seen distinguishing one part of the cytoplasm from another.

Cleavage. Although I obtained many hundred eggs and larvae, I only succeeded in one instance in finding the earliest stages. One lot contained a few unsegmented eggs and several in early cleavage (four, eight, sixteen cells). The material was insufficient for a study of the cell lineage.

First cleavage. Bateson '84 (p. 209) says of the early cleavage: "The first furrow is formed in a median plane, dividing the ovum into two equal parts. It passes to a considerable depth. With regard to subsequent segmentation I have no certain observations; for though some of the ova divided into four and eight nearly equal parts, these were obtained by artificial fertilization, and the process of division was afterwards continued in an entirely abnormal manner as mentioned above. Judging, however, from the characters of the blastosphere, and from the fact that yolk granules are uniformly distributed through the whole tissue, there can be little doubt that the segmentation is regular and complete."

I am able to verify the above observations in regard to the first cleavage. (Fig. 3, pl. 5.)

Second cleavage. (Fig. 4, pl. 5.) The second cleavage is also equal, the blastomeres being arranged at first in perfect radial symmetry. In most cases this symmetry seems to persist, but in a few there is a slight irregularity. This irregularity was at first attributed to displacement due to manipulation. While this may

be the case it was more likely normal, especially in view of the position of the blastomeres of some eggs of the third cleavage. Wilson '94 has called attention to the same thing in Amphioxus: "Slight as they are," says this author, "they deserve attentive consideration, for they give, I believe, a key to the more considerable deviations of later stages."

Third cleavage. (Fig. 5.) The third cleavage is unequal and is of especial interest because of its similarity to that of Amphioxus. The blastomeres of the upper pole are smaller than those of the lower. The difference in size between those of the two poles is somewhat less than that shown by Wilson for Amphioxus; otherwise the two eggs are much alike even to the exception to the usual bi-lateral form of segmentation, for as in Amphioxus there occurs a deviation from the typical arrangement of blastomeres into the spiral form described by Wilson.

The slight irregularity noted in the second cleavage and the spiral form in the third cleavage were observed on preserved material. I am therefore unable to say whether or not the irregular second cleavage of *D. pusillus* gives rise, as Wilson found for Amphioxus, to the spiral third cleavage. The early cleavage stages of the two animals being thus far so much alike, and also in other respects to be described, suggest that they may be found to be alike in this particular also.

Fourth cleavage. (Fig. 6.) The typical fourth cleavage is shown in fig. 6. Here it will be seen that the cleavage is bi-lateral. All eggs observed in this stage, except one, were of this form. This one exception corresponds to Wilson's mixed form of cleavage.

Fifth cleavage. (Fig. 7.) In the fifth cleavage another point of similarity between *D. pusillus* and Amphioxus is to be observed: the presence of a cleavage pore. This and the bi-lateral form of cleavage is shown in fig. 7. A large per cent. of eggs of this stage and stages immediately following possessed cleavage pores.

Sixth and subsequent cleavages. The sixth and subsequent cleavages do not show clearly a bi-lateral symmetry. Two of these stages are shown in figs. 8, 9, pl. 5.

Comparison of D. pusillus with Amphioxus. Although my

observations as above recorded were made upon few individuals they are sufficient to warrant pointing out the great similarity between the early cleavage of this animal and Amphioxus. A reëxamination of plenty of material and a careful study of the cell-lineage of *D. pusillus* would no doubt show a greater likeness. The points of similarity are:

(*a*) Bi-lateral form of cleavage, as a rule.

(*b*) Occasional variation from this into spiral, and perhaps into radial and mixed cleavage.

(*c*) Frequent occurrence of a cleavage pore.

(*d*) Gradual obliteration, in later stages, of bi-lateral symmetry.

The points of difference are:

(*a*) Absence of radial cleavage in *D. pusillus*. But since there was one instance of mixed cleavage, it is not unlikely that in a large number of individuals in early cleavage some of this form might be found.

(*b*) Less difference in the size of the blastomeres of the two poles of the third cleavage in *D. pusillus* than in Amphioxus. This point, however, is unessential since the yolk is uniformly distributed in the eggs of both animals, and the stages subsequent to the third cleavage are alike as far as can be shown with the material at hand.

Comparison of D. pusillus and Amphioxus with Ascidia (Ciona intestinalis) in their early cleavage. Castle and Conklin were able to recognize that the unsegmented ovum of Ascidia is made up of two unlike hemispheres, one richer in yolk and the other richer in protoplasm. Castle '96 concludes: "The form and rate of cleavage are therefore manifestly predetermined by the internal constitution of the ovum." In the Enteropneust egg (*D. pusillus*) and in the egg of Amphioxus no such distribution of yolk and protoplasm occurs.

With reference to symmetry of cleavage Castle '96 (p. 233) says: "Wilson '94 observed that the cleavage of Amphioxus showed all gradations between a perfectly radial, a bi-lateral, and even a spiral form; and raised a query whether the same might not be true for Ascidians. In Ciona at least this does not seem to be the case. I have never observed an instance of deviation

from the regular mode of cleavage described in the foregoing paper." By "regular mode" he means bi-lateral. He adds further: "In having a perfectly definite and stereotyped manner of cleavage, the Ascidian egg resembles more closely the egg of Annelids, Mollusks, and the great majority of invertebrates than it does Amphioxus and the vertebrates, notwithstanding that the *end product* of cleavage shows unmistakably the now generally admitted closer affinity of the tunicates with the latter group of animals."

One must conclude from this and from what has been indicated in the comparison of *D. pusillus* with Amphioxus that, in so far as resemblance in cleavage may be relied upon for determining affinities, there is a closer relation between these two animals than between Ascidia (Ciona) and Amphioxus.

Blastula. The blastocoele appears as a segmentation cavity as early as the fourth cleavage, so that it is difficult to set apart the stages of cleavage, just described, from the blastula.

I shall regard the stage just succeeding that shown in fig. 9, as the early blastula stage, for it corresponds to the earliest stage that Bateson found beyond the first cleavage and which he calls the blastosphere. He describes it as spherical, with opaque walls, though "the outline of cells composing them could be faintly distinguished in a surface view."

I did not find among my living stages of the blastula the elliptical form described by him for the later stages; but in preservation some became elliptical. I did, however, observe the slightly flattened condition which he describes as just preceding gastrulation.

Gastrula. Estimated from the time eggs were taken from the burrow when segmentation no doubt was beginning, until the first evidence of gastrulation, about twenty hours elapsed (figs. 10 and 11). Bateson's account of external changes of this period agrees largely with my own observations.

The flattened condition of the gastrula remains but for a short time. Before the ring of cilia appears the gastrula is nearly spherical. In this respect it differs from *B. kowalevskii.*

The time between the beginning of gastrulation and the appearance of cilia is about twelve hours. The blastopore can no

longer be seen from the surface but sections show that it does not completely close until about six hours later.

Larva within the egg-capsule. The larval period may be said to begin with the closure of the blastopore and elongation of the body. This elongation is at right angles to the plane of the ciliary band. I was, unfortunately, not able to determine the relation of the axis of the embryo to the first cleavage plane.

The most important changes that take place are: growth in length, enlargement of the ciliary band, appearance of the posterior collar groove and later of the anterior groove; and development of the anterior, or apical cilia. (Figs. 13, 14, pl. 6.) As these changes are fully described by Bateson '84 and are so closely repeated in the present species I need not here discuss them.

Period II.

The larva remains through this period, in external appearance, just as when leaving the egg, except perhaps for a slight elongation of the body. (Fig. 15, pl. 6.) The significance of this quiescent stage has already been discussed in another connection.

Period III.

Like period I, this period is marked by many changes: further elongation of body, both of proboscis and body proper; appearance of gill openings; disappearance of apical cilia, and, later, reduction of the ciliary band; increase in diameter and width of collar. (Fig. 16, pl. 6.) I have nothing to add to Bateson's (pp. 211-213) full description of the external appearance of the stages of this period. My own observations, except for slight details, agree with his.

Internal Features.—Period I.

Blastula. The first internal change to be noticed is in the latter part of this period. The cells forming that portion of the blastosphere which is to be invaginated (endodermal portion) are somewhat irregular, having rounded ends projecting unevenly into the blastocoele. (Fig. 18, pl. 7.) They are relatively narrower than the cells of the opposite portion of the blastosphere

(ectodermal portion), probably indicating more rapid cell division in this region.

Numerous large round cells, many of them in mitosis, are to be seen near or at the surface of both the ectodermal and endodermal portions of the blastosphere. These cells are further distinguished from the remaining cells by having different staining properties of the cytoplasm. One of them is shown in fig. 18, *g. c.* None were noticed earlier.

Bateson found a greater difference between the ectodermal and endodermal portions of the blastosphere than I have just described. He did not, however, notice the presence of the round cells, above mentioned, which are very conspicuous in this and later stages of *D. pusillus.*

Gastrula. The gastrula is formed by the invagination of the endodermal portion of the blastosphere, and elongation in the direction of a line passing through the center of the blastopore and opposite pole. As elongation proceeds the endoderm approaches the ectoderm until the two layers meet. At the same time the blastopore is closing.

Fig. 19, pl. 7, shows the early stage of gastrulation before elongation. It will be noticed that the endoderm is somewhat thinner than the ectoderm, and that there is less difference in the histological character of the cells than in the stage just preceding invagination. The rounded ends of the endodermal cells and indications of their being amoeboid, as described by Bateson '84 (p. 213), I was unable to find.

Fig. 20 is a longitudinal section through the blastopore at the last stage of gastrulation. Here the blastopore is about closed, and the two layers are adjacent. The cells of the region of the blastopore are irregular and in rapid division as indicated by the numerous nuclei. The ectodermal part of the blastoporic rim is already in process of fusion. Later the endodermal part fuses, and thus the blastopore is completely closed. The ectoderm and endoderm of this region remain coalescent for a time (fig. 21), but finally separate (fig. 22, pl. 7).

In this manner the gastrula passes into what Bateson (p. 215) calls a "two-walled cylinder," the outside wall of which is the ectoderm, and the inside the endoderm. With the exception

already noted, my observations on this stage agree with Bateson's account. I have, therefore, omitted many details.

Mesoderm and body cavities. Bateson (p. 214) says of the two-layer stage just described: "The hypoblast of the middle region is seen to be more columnar in character than that of the anterior region, while the other appearances are the same." Fig. 22 shows this condition. It will be noticed that the cells of the extreme anterior are somewhat shortened. The cells at the transition from the anterior to the middle region tend to lose their columnar character and to become irregular. Here, as we shall see, is the beginning of a series of changes in the endodermal cylinder which is to give rise to the mesoderm.

Since Spengel '04 associates the formation of the mouth with the origin of the mesoderm in tornaria it may be worth while to state that according to Bateson's observations on *B. Kowalevskii* and my own on *D. pusillus* the mouth does not appear until after the mesoderm is formed.

By the time the two layers in the blastoporic region have become separated, that portion of the endoderm which has just been described as composed of irregular cells (fig. 22) has projected outward and backward somewhat, thus partially separating the archenteron into anterior and posterior parts. The former will be referred to as "anterior body cavity" (Bateson '84, p. 216). This stage of development is shown in fig. 23, pl. 8. It will be seen that the cells of the walls of the anterior cavity are becoming irregular, especially on the sides, and that some cells are being budded off into the cavity. Rapid growth and redisposition of cells continue until the condition shown in fig. 24 is reached. Here the anterior body cavity although irregular shows the beginning of a lateral and backward projection. The walls of the anterior body cavity and those of the archenteron are sharply differentiated in character of their cells. The archenteron will henceforth be referred to as *enteron*.

The lateral backward projections of the walls of the anterior body cavity continue to grow. The next two stages are shown in fig. 25 and fig. 26, pl. 8.

It must be here noted that the backward growth is not only lateral, but, for a short distance, dorsal as well. There is no

ventral extension, so that the mesoderm forms a broken ring around the anterior extremity of the enteron (fig. 27). From this point the mesodermal growth is confined to the sides. (See quotation from Bateson.)

The following description refers exclusively to the lateral backward growth of the mesoderm. In the section represented in fig. 24, pl. 8, it will be seen that the walls of the enteron are completely separated from the anterior body cavity except at one point. Complete separation is seen in stages represented by figs. 27 and 28. The walls of the anterior body cavity may now be called mesoderm.[2] The edges of the anterior portion of the enteric walls are approaching, leaving a small oblong communication (oblong dorso-ventrally) between the two cavities.

The growth of the mesoderm backward is taking place wedge-wise between the walls of the enteron and the ectoderm. The cells of the edge are irregular, tending somewhat to flatness at its narrow extremity. In this way the mesoderm continues to grow backward, the wedge of cells (as seen in longitudinal section) becoming somewhat longer and thinner, and reaching beyond the collar region. This stage of development is shown in fig. 25. At a little later period an important change takes place. The mass of cells extending backward between the enteric wall and the ectoderm loses its wedge-shape in longitudinal section. At a point corresponding to the anterior collar groove, the mass of cells is slightly constricted. In the collar region corresponding in longitudinal extent to the collar, the cells form two layers. Posterior to this region the mesoderm continues for a short distance as a single layer of somewhat flattened cells. (Fig. 26.) This is the beginning of the middle body cavity.

The mesoderm grows backward until it almost reaches the posterior extremity of the enteron. In the meantime a second constriction occurs at a point corresponding to the posterior groove of the collar (fig. 28, pl. 8). Posterior to this constriction the mesoderm forms two layers just as described above for the collar region.

In this manner the middle and posterior body cavities arise

[2] The term mesoderm has already been used in reference to the portion of this region which is reflected backward.

from the mesoderm. Their walls are one-cell deep, the cells becoming flattened. For a while the three body cavities, anterior, middle, and posterior, are continuous, though marked off by the constrictions already described. Fig. 29, pl. 8, shows the relation of these cavities to one another at this stage. Subsequently the constrictions deepen until finally they completely separate the cavities.

Prior to this period the middle and posterior cavities have extended ventrally somewhat, but more dorsally. This growth continues concomitantly with the later stages of longitudinal growth just described. They extend dorsally, meeting at the mid-dorsal line, but ventrally they do not quite meet.

As the above account of the origin of the middle and posterior body cavities in *D. pusillus* is at absolute variance with Bateson's description of the origin of these structures in *B. kowalevskii*, and with his diagram, familiar in text-books, I wish to review his account somewhat fully.

After describing the stage corresponding to that in *D. pusillus* shown in fig. 23, pl. 8, he says: "The mesoblast arises at this period of development. It is formed directly by differentiation of cells belonging to the archenteron. These differentiations occur in five regions. The first comprises a median and primitively-unpaired tract in the anterior end, which forms the lining of the body cavity of the praeoral lobe. Behind this anterior body cavity a pair of mesoblastic differentiations occur in the region of the collar, constituting lateral outgrowths of the archenteric walls, each containing a cavity which communicates directly with the cavity of the archenteron. Behind these, again, is another pair of regular archenteric diverticula, in the region of the trunk." He refers at this point to his well known diagram illustrating his description.

He then describes in detail (pp. 141-142) the development of the anterior body cavity. The latter part of his description (pp. 218-219) is as follows:

"Now, since the anterior body cavity is continued behind the end of the gut on all sides excepting the ventral, it is crescentic in shape, the concavity being directed downwards. This appearance exists only for a short distance. Behind it the continuity

across the dorsal surface ceases, and *the mesoblast exists as a pair of small, hollow cavities at the dorso-lateral sides of the gut, which is here much more fully developed, occupying most of the space enclosed by the epiblast. Still farther backward the cavities in these two mesoblastic tracts close up, and their walls are continued for a short distance as two solid cords of cells, and then disappear.*

"The mesoblast of the anterior body cavity is, therefore, formed directly from the walls of the hypoblast, which occupied the same situation. It is separated off from it by a process of constriction in the region of the external groove, dividing the proboscis from the collar. While this process of constriction is being carried out, *the pouch of mesoblast grows backwards, surrounding the gut except on the ventral surface, but especially forming the hollow horns.*" (Italics mine.)

The description which I have just quoted agrees substantially with my own observations of the origin and first stages of development of the mesoblast in its relation to the anterior body cavity. The portions of his description of the lateral backward growths of the mesoblast which I have italicized is almost an exact account of the stage which I have shown in fig. 26, and I believe must correspond to it. As I have shown, the mesoderm already growing backwards continues to do so at the sides, finally *forming* the *middle* and *posterior body cavities*. This conclusion is based on an examination of a large number of sections (about one hundred and fifty series of sections), a typical series of which I have shown in my figures. *Nowhere have I seen any indication of a communication between any one of the middle or posterior cavities with the enteric canal.* Neither have I seen any evidence of delamination of the enteric wall. Throughout all the stages, from the two-walled cylinder to that of the fully formed body cavities, the walls of the enteron in the region of the middle and posterior body cavities show no histological difference from other parts of the wall. Whereas the cells bounding these cavities are very different from the cells making up the wall of the enteron.

Concerning the connection between the middle body cavities and the archenteron Bateson '84 (p. 220) says: "This condition is only visible in a very few of the larvae, and may possibly be

due to the action of reagents. Since, however, the middle mesoblastic tracts in Tornaria are said to be archenteric diverticula (Spengel, etc.), it seems more likely that the rarity of their occurrence is due to the shortness of the time for which they are present."

Of the connection between the posterior body cavities and the archenteron he is more certain. He says (p. 221): "These mesoblastic pouches open by large foramina into the lumen of the gut." No such large foramina exist in any stage that I have studied in *D. pusillus*. Although Spengel '77, several years before Bateson's paper, held that the middle mesoblastic tracts in Tornaria are "archenteric diverticula," he later modified this view, for he says (Spengel '94, p. 431): "dass die beiden Cölome jeder Seite aus einer gemeinschaftlichen Anlage hervorgehen, die später in zwei Theile zerfällt."

I cannot but think that Bateson failed to notice the connecting links between the mesoderm of the anterior body cavities and that of the other cavities, for his observations of the early backward growth of the mesoderm, as well as of the cavities after being formed, agree with mine. Indeed, his fig. 36 shows a communication, or at least a close connection, between the middle and posterior body cavities just as I have shown in my fig. 28. The only essential difference between his figure and mine will be seen to be in the definite line which he has drawn separating the anterior from the middle body cavity. Such a separation does not occur in my sections of the same stage.

Furthermore the archenteric walls in the region of the middle and posterior cavities at no time show any evidences of outpocketing. If these cavities were outgrowths of the archenteric wall one would expect to find evidences of this growth in the disposition of the cells of these regions. In the early stages of the anterior cavity the cells of the portion of the archenteron giving rise to it are irregular both as to shape and arrangement. The same condition is observed at the blastopore at the time of its closure. But no such irregularity is ever noticed in the archenteric walls, where according to Bateson the middle and posterior outgrowths occur.

Morgan '94 does not accept Bateson's account of the origin

of the second and third body cavities as will be seen from the following (p. 70): "The collar cavities are said to arise by a pair of lateral evaginations from the archenteron. For the present I accept this account of the origin of the second pair only tentatively. The evidence furnished by Bateson does not seem to me conclusive for accepting his statement. I think the phenomena could be explained by a process of delamination or migration, and a subsequent opening (or perhaps the small openings are artifacts)."

If one may judge from his descriptions and figures, Bateson relied in his studies mainly upon transverse sections, whereas the relation of the cavities to one another may be more certainly followed on horizontal longitudinal sections. But these suggestions hardly suffice to harmonize our observations. The other alternative is that *B. kowalevskii* and *D. pusillus*, though so much alike in most respects, differ widely in the origin and development of their middle and posterior body cavities. But this is hardly probable.

Gland cells. One characteristic of the Enteropneusta is the presence of numerous unicellular glands in the epidermis. Allusion has already been made to the very active secretion of these glands which occurs in period III. I have also called attention to certain large round cells which make their appearance on the periphery of the blastula.

Those that happen to be on the endodermal portion of the blastula are invaginated during gastrulation. They persist a while in the endoderm, but I was unable to determine their subsequent fate.

The cells which are in the ectoderm increase in number throughout the subsequent stages. During the latter part of period I some of these are made deep blue by Mallory stain, indicating the mucous character of their contents.

In period II they become numerous in the collar region, and at the two extremities. Some are empty; others are full of secretion.

In the early part of period III the number in the collar region is so great as to form an almost continuous layer. Here, in Mallory-stained sections, the collar presents a deep blue border,

with here and there light spots indicating the position of cells from which secretion has been discharged.

OCCURRENCE OF HALF EMBRYOS AND DOUBLE EMBRYOS.

The blastomeres of the early cleavages are loosely held together. This fact may account for the appearance of various small embryos. No careful study was made of them; indeed a great many were destroyed or not preserved. From the few notes I made the following may be of interest, particularly in view of the recent studies in the development of egg fragments.

The occurrence of what may be called half embryos was noted in several stages. The earliest was where two blastomeres of the four-celled stage had been destroyed. The next stage observed consisted of eight blastomeres. This stage corresponds to the third cleavage except in the smaller size of the blastomeres. Another stage was an early blastula about half normal size. Within the egg capsule were the disintegrating remains of a blastomere, probably the companion of the one that had developed. The latest stage observed was one where the ciliary band had appeared. It was small but otherwise normal. In the egg capsule was a disintegrating blastomere.

The occurrence of double embryos was observed in a few stages, but none later than the blastula. The embryos seemed normal except in size.

These observations would indicate that isolated blastomeres in *D. pusillus* may develop into embryos, as they are known to be able to do in Amphioxus and some other animals.

COMPARISON OF D. PUSILLUS WITH AMPHIOXUS WITH REFERENCE TO ORIGIN OF BODY CAVITIES.

Since Bateson called attention to certain points of similarity between Balanoglossus and Amphioxus various attempts have been made to further homologize the two animals. In these discussions one point has been made much of, especially by MacBride '98, *viz.*, the similar origin of the body cavities. He says: "The mesoderm originates in Amphioxus as a series of true gut

pouches, *viz.,* one anterior unpaired pouch and two pairs of lateral pouches. Of these, the first divides to form the two head cavities; the anterior pair give rise to the first pair of myotomes, and in addition to two long canals extending back ventrally; the posterior pair are gradually separated from the gut, and pari passu divided into a series of myotomes. The whole process of mesoderm formation is therefore referable to the type found in Balanoglossus, the main difference being that the pouch corresponding to the trunk coelom of Balanoglossus becomes segmented." Pp. 606-607.

He reproduces, though somewhat modified, the diagram which Bateson '84 (fig. 40) used to illustrate the body cavities of Balanoglossus. When seen side by side, Bateson's diagram of the body cavities of Balanoglossus and MacBride's diagram of the body cavities of Amphioxus are strikingly similar. If one were to judge by these the homology of the cavities of the two animals would seem to be well established.

Recently MacBride's work has been questioned. Cerfontaine, '05, says of MacBride's contention that in Amphioxus the mesoblast occurs in five diverticula: "Je dirai dès à présent, que, dan mes nombreuses préparations je n'ai jamais vu, quoi que ce soit, qui puisse avoir des rapports avec une semblable évolution du mésoblaste chez l'Amphioxus, et je dois encore une fois répéter que certaines figures, qui accompagnent le memoire de MacBride dénotent, évidemment, une mauvaise conservation du matérial." p. 364. "L'ébauche du mésoblaste, existe sur tout le pourtour l'ébauche notochorde. Cette ébauche du mésoblaste, au moment de l'achèvement des phénomènes de gastrulation, presente, avec l'orifice d'invagination des rapports tels, qu'on doit distinguer chez l'Amphioxus, mangré l'absence des cellules polaires de Hatschek, un mésoblaste gastral et un mésoblaste prostomial." p. 389. With such a disagreement as to the origin of the mesoderm in Amphioxus it would be difficult to homologize the body cavities of this animal and those of Balanoglossus even if Bateson's account of the latter be accepted. But the difficulty grows into an impossibility if I have made my case as to the origin of the cavities of *D. pusillus* and as to the improbability that they arise differently in *D. kowalevskii* from what they do in *D. pusillus.*

If we are looking for types having a development of body cavities similar to that found in *D. pusillus* we must take into consideration Annelids and Molluscs. In both of these groups the general plan of mesodermal development as shown, for example, by Wilson, for Annelids and by Conklin for Molluscs may be briefly stated as follows: The development of body cavities is from in front backwards. The mesodermal bands posterior to cavities already formed are undifferentiated and "new cell material continues to be formed here in the vicinity of the primitive mesoderm cells."

The development of the body cavities in *D. pusillus,* as I have shown, follows in a *very general* way the above plan. But I do not wish in making this comparison to suggest any homology. On the contrary, I wish rather to emphasize the great difficulty in the present state of our knowledge of establishing any homologies whatever for these structures.

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ABBREVIATIONS USED IN THE FIGURES.

a. Archenteric cavity.

a.m. Anlage of mesoderm.

b.c. 1, 2, and 3: first, second, and third body cavities respectively.

ec. Ectoderm.

en. Endoderm.

ent. Enteron.

g.c. Gland cell.

m. Mesoderm.

m.f. Muscle fibers.

n. Nerve cord.

EXPLANATION OF PLATES.

PLATE 4.

Fig. 1 shows adult animal partly in mud, with one end (anterior lifted and turned aside showing burrow and the eggs clinging to one side—the unbroken side of the burrow). × 1, sketched from life.

PLATE 5.

Fig. 2. Unsegmented egg, actual size 264μ

Fig. 3. First cleavage, greatest diameter 420μ

Fig. 4. Second cleavage, greatest diameter 420μ

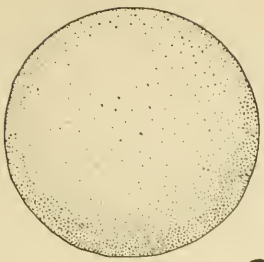
Fig. 5. Third cleavage, greatest diameter 360μ

Fig. 6. Fourth cleavage, greatest diameter 360μ

Fig. 7. Fifth cleavage. Cleavage pore shown, 384μ

Fig. 8. Sixth cleavage. Cleavage pore shown, 384μ

Fig. 9. Seventh cleavage, 360μ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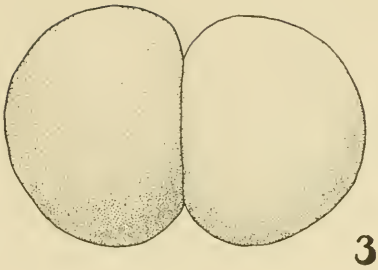
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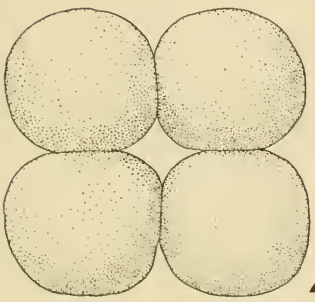
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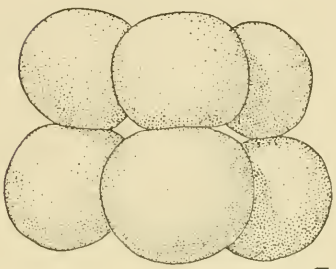
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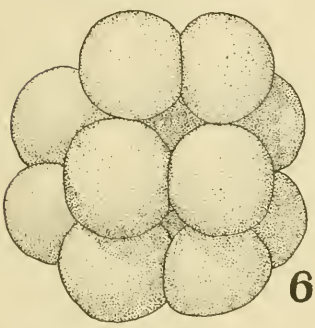
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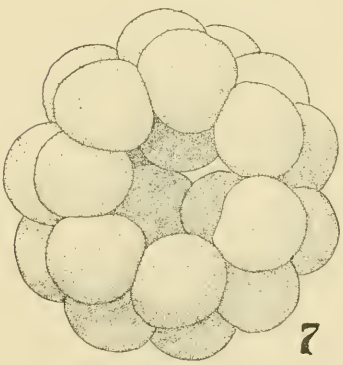
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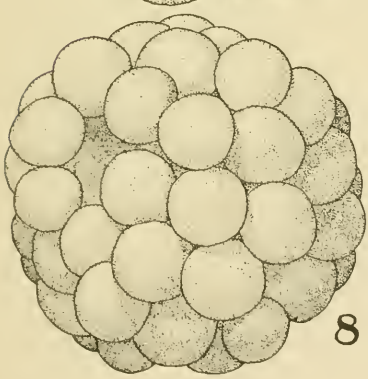
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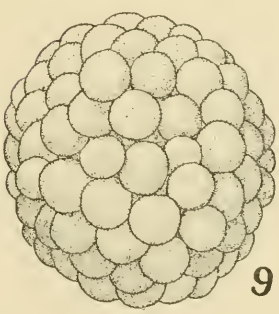
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PLATE 6.

Fig. 10. Gastrula, early stage. (a) Looking toward blastopore. (b) Side view, 300μ

Fig. 11. Gastrula, late stage, looking toward the blastopore, 300μ

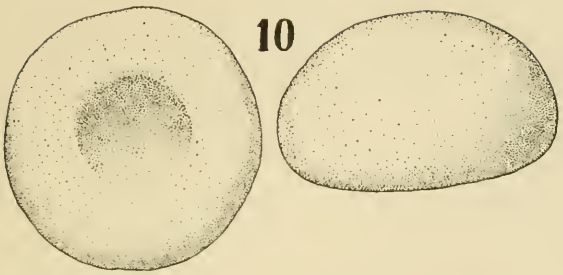
Fig. 12. Period I soon after appearance of ciliary band, long axis, 300μ

Fig. 13. Period I soon after appearance of groove, long axis 336μ

Fig. 14. Period I at time of hatching, 384μ

Fig. 15. Period II, latter part, long axis 384μ (partly contracted).

Fig. 16. Period III, second phase, long axis 540μ (average).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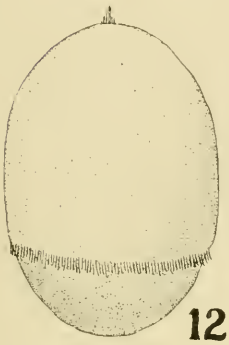
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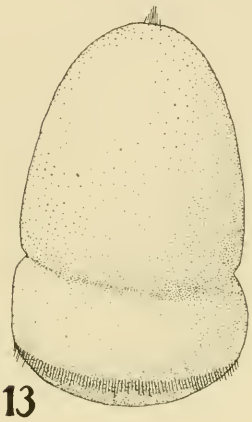
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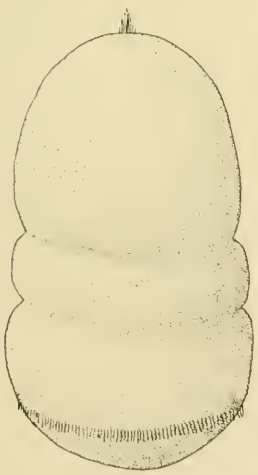
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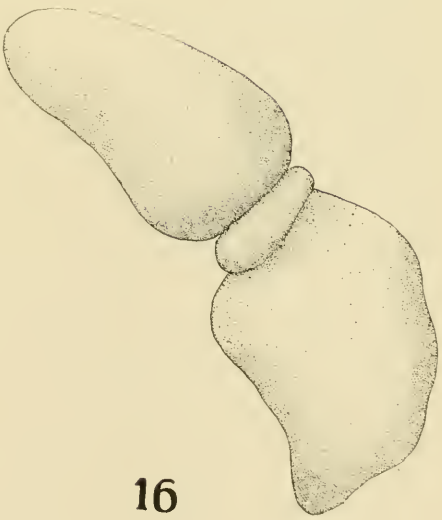
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PLATE 7.

Fig. 17. a. b. c. Diagrams showing escape of larva from egg capsule. × 190.

Fig. 18. Section of blastula. × 190.

Fig. 19. Section of gastrula, early stage. × 190.

Fig. 20. Section of gastrula just before closure of blastopore. × 190.

Fig. 21. Section of larva immediately succeeding closure of blastopore. × 190.

Fig. 22. Sagittal section of larva at the beginning of two-walled cylinder stage, showing rapid growth of cells in archenteric wall. × 190.

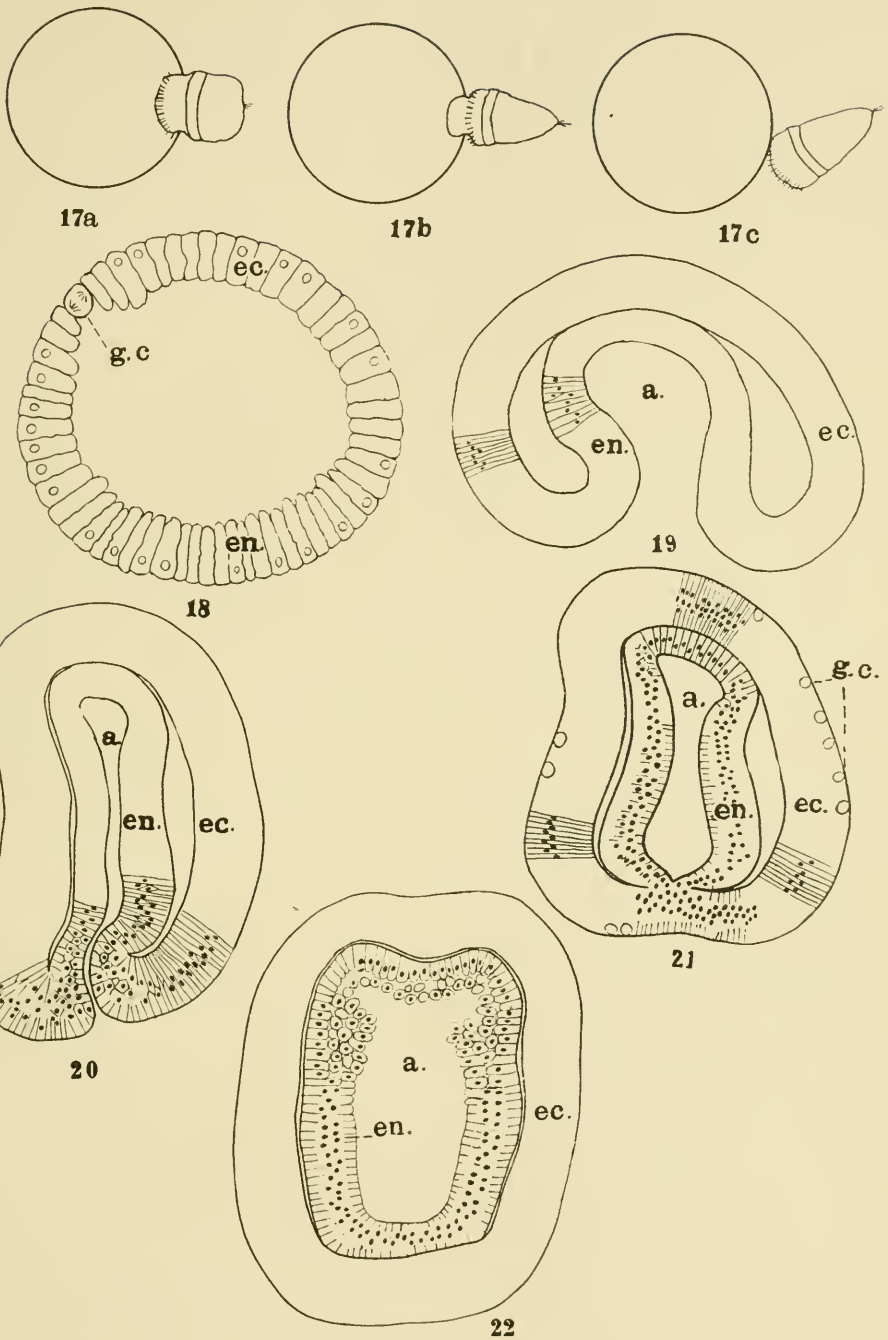
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PLATE 8.

Fig. 23. Horizontal section of somewhat older larva than that represented in fig. 22. Here further irregularity appears among cells at anterior of archenteric wall. × 190.

Fig. 24. Horizontal section of larva. Here the irregular disposition of cells indicated in fig. 23 is still shown but with a tendency to grow backward between the ectoderm and endoderm or archenteric wall. This wedge of cells is the anlage of the mesoderm. × 190.

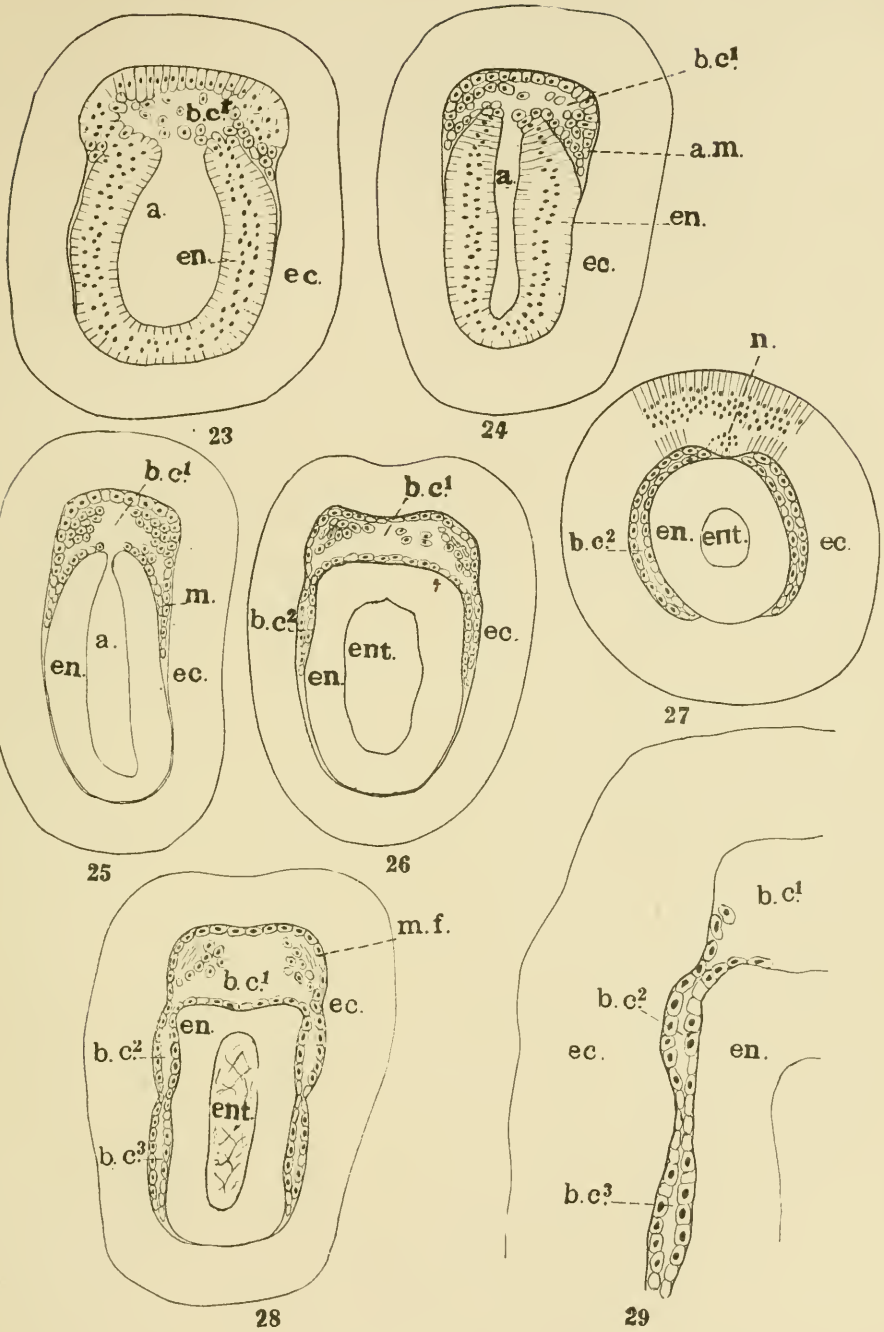
Fig. 25. Horizontal section of larva. Here the wedge of cells has reached beyond the collar region. × 190.

Fig. 26. Horizontal section of larva showing formation of second body cavity. × 190.

Fig. 27. Transverse section of larva somewhat older than that figured in 26. Section cuts across second body cavity. × 190.

Fig. 28. Horizontal section of larva showing formation of third body cavity, and the relation of the three body cavities to one another. × 190.

Fig. 29. Part of similar section of same larva figured in 28 but more enlarged. This figure shows communication between cavities 1 and 2, and 3. × 300.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NOTES ON TWO AMPHIPODS OF THE GENUS COROPHIUM FROM THE PACIFIC COAST

BY

J. CHESTER BRADLEY

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In 1857 Mr. William Stimpson, the distinguished zoologist of the North Pacific Exploring Expedition, 1853-1856, published brief descriptions, without figures, of two amphipods, *Corophium spinicorne* and *C. salmonis*, from the Pacific Coast, the former from the Bay of San Francisco, the latter from the stomach of an unidentified species of salmon from Puget Sound.

The collections at the University of California contain specimens of *Corophium* which, in so far as can be determined by Stimpson's brief and inadequate descriptions, belong to the above named species.

This material consists of about two dozen specimens, mostly females, of *Corophium spinicorne* from the type locality, San Francisco Bay, and about six hundred specimens of *C. salmonis* taken from the stomachs of young salmon in Alaskan waters. It is interesting that the types of this species were also obtained from the stomachs of salmon from Puget Sound.

In Stebbing's ('88) exhaustive review of amphipod literature he makes the following comment upon these two species described by Stimpson.

"*Corophium spinicorne* Stimpson, was apparently unknown to Spence Bate, as in the Brit. Mus. Catal. he makes a new *Corophium spinicorne*, which Boeck identifies with *Corophium crassi-*

cornc Bruzelius. *Corophium salmonis*, which Stimpson took 'not in a very good state of preservation' out of the stomach of a salmon, had almost better have been left there, instead of being drawn forth to create a very indistinct species."

Later Della Valle ('93) in his Naples monograph relegates Stimpson's species to the limbo of imperfectly defined species with the laconic remark regarding the description of *C. spinicorne* "Cita caratteri communi a tutti i Corophium," and regarding *C. salmonis* "Naturalamente, tutto questo non basta a far distinguere a la n. sp."

Later in his monograph of the Gammaridea Stebbing ('06) accepts twelve species as valid and in the appendix adds four more species of *Corophium*, but places *spinicorne* and *salmonis* among those "rejected" without remark.

Since these species appear to be distinct from others of the genus and their types have apparently been lost, and since their published descriptions are most inadequate, it has seemed worth while to publish here detailed figures and descriptions of the two species. The work has been done and the drawings made under the direction of Prof. C. A. Kofoid, to whom I am also indebted for the privilege of studying the material on which it is based, and for the expenditure of much time and labor in the preparation of the manuscript.

Stimpson's ('57) original description of *C. spinicorne* reads as follows:

"*Corophium spinicorne* St. Inferior antennae half as long as the body, without flagella, and with a large curved, sharp pointed, spine at the inferior extremity of the very thick third article. Superior antennae nearly as long as the inferior ones. Feet with plumose hairs; those of the first pair with minute subcheliform hands, palms transverse, third and fourth articles with long setae along the inferior edge. Feet of the second pair simple, but with the third and fourth articles conjoined laterally, as if forming a hand; the fourth article being placed inferiorly and fringed with long hairs. Caudal stylets as in *C. longicorne*, except that the external ramus in the second pair is not cultriform. Color, brownish, darkest at the head, with transverse bands of light yellow corresponding to the articulations. Antennae brownish.

Lenth 0.4 inch. Found among confervae, etc., in the salt marshes on the shores of San Francisco Bay."

In a subsequent paper Stimpson ('57a) repeats the description of *C. spinicorne* and adds that of *C. salmonis* as follows:

"In examining anatomically a species of salmon from Puget Sound, in the museum of the Smithsonian Institute, the stomach was found to be filled with Amphipods, chiefly a species of *Corophium*. The specimens were not in a very good state of preservation, but enough remained to show that although agreeing with the preceding species *(spinicorne)* in most characters, particularly in the spines of the antennae and the hairiness of the feet, they are yet specifically distinct. The body is rather more elongated and depressed than in *spinicorne*, the inferior antennae are much longer, and the superior ones smaller. The color is reddish-purple."

KEY TO THE SPECIES OF COROPHIUM.

This key includes all the species accepted by Stebbing ('06) including those in the appendix, except *C. maeoticum* Sowinsky ('98, Bull. Acad. St. Petersb., vol. 8, p. 362; pl. 1, figs. 1-5). It is based on the synopsis given by Stebbing ('06), but modified so as to exclude secondary sexual characters, such especially as are found in the antennae.

1. Abdominal segments 4-6 distinct 2
   Abdominal segments 4-6 fused 15
2. Ramus of third uropod oval 3
   Ramus of third uropod parallel-sided 9
3. Second antennae chelate 4
   Second antennae not chelate 5
4. Abdominal segments 4-6 smooth ..... **C. chelicorne** Sars.
   Abdominal segments 4-6 spinulose ..... **C. spinulosum** Sars.
5. Dactyl of second gnathopod simple, slender; propodus of first peraeopod slightly over one-third as broad as long; telson obtusely pointed ..... **C. volutator** Pallas.
   Dactyl of second gnathopod toothed 6
6. Dactyl of second gnathopod long and slender, four to seven times as long as greatest breadth, bearing 1 to 5 small recumbent teeth besides a long apical tooth 7
   Dactyl of second gnathopod very stout, about as broad as long, with three large recurved teeth, the third forming the apex of the dactyl ..... **C. triaenonyx** Stebbing.

7. Propodus of first peraeopod over one-half as broad as long 8
   Propodus of first peraeopod only one-fourth as broad as long; dactyl of second gnathopod with three small teeth beneath ..... **C. nobile** Sars.
8. Dactyl of second gnathopod with five teeth beneath; propodus of fifth peraeopod twice as long as the dactyl..**C. salmonis** Stimpson.
   Dactyl of second gnathopod with two teeth beneath; propodus of fifth peraeopod nearly four times as long as the dactyl ..... **C. cylindricum** Say.
9. Ramus of third uropod linear 10
   Ramus of third uropod not linear 11
10. Dactyl of second gnathopod simple; first antennae of the male with a hooked process on the basal segment. **C. runcicorne** Della Valle.
    Dactyl of second gnathopod toothed at apex; first antennae of the male with the basal segment simple ..... **C. affine** Bruzelius.
11. Carpus of fifth peraeopod almost one-half as broad as long ..... **C. mucronatum** Sars.
    Carpus of fifth peraeopod three and one-half to four times as long as broad 12
12. Ramus of the third uropod without a terminal spine 13
    Ramus of the third uropod with a terminal spine....**C. monodon** Sars.
13. Rami of the second uropoda about normally, sub-equally, robust, their lateral edges bearing 3 to 5 spines and each ramus with three apical spines 14
    Outer ramus of second uropod stout, inner very slender; the outer unarmed, except for one apical spine, the inner with one mesal and two apical spines ..... **C. spinicorne** Stimpson.
14. Outer edge of outer ramus of second uropod with five spines; inner edge of inner ramus with four spines; ultimate segment of peduncle of second antennae apically produced..**C. robustum** Sars.
    Outer edge of outer ramus of second uropoda with three spines; inner edge of inner ramus with two spines; ultimate segment of peduncle of second antennae apically not produced ..... **C. curvispinum** Sars.
15. Cephalon without any rostrum ..... **C. bonelli Milne** Edwards.
    Cephalon with a rostrum 16
16. Dactyl of both first and second gnathopods simple ..... **C. crassicorne** Bruzelius.
    Dactyl of first gnathopod bifid, of second gnathopod trifid, at apex ..... **C. acheruzicum** A. Costa.

Corophium spinicorne Stimpson.

Pls. 9, figs. 1-11; 10, figs. 12-19; 13, figs. 36, 37.

Second antennae of the adult female (pl. 9, fig. 1) about one third longer than the first (pl. 9, fig. 2). Peduncle of the first pair with the basal segment stout, equal to the second, armed with

a pair of spines below and one fourth of the way toward the apex with another spine; third segment not half as long as second. Flagellum sub-equal to peduncle, the basal segments shorter than those beyond. Second antennae (pl. 9, fig. 1) very stout, the first segment with a pyramidal process on the lower margin; the second with a small spine near the apex of the lower margin; the penultimate produced into a large slightly recurved spine at the distal end of the lower margin, without any teeth above its apex; its lower margin at a distinct angle to that of the segment bearing it. The ultimate segment subcylindrical, a little more than one-third as thick as the preceding, produced at apex into a lobe on one side, extending a little less than one-third of the length of the first segment of the flagellum, the basal half of the lower margin bearing two stout spines. Flagellum shorter than the ultimate segment of the peduncle, three-segmented, the first segment over four times longer than the second, the third minute, bearing two curved terminal spines and numerous setae. In a young female (pl. 9, fig. 6) the basal segment of the first antennae is broader, and in addition to the small basal spine there are three long and slender spines; the flagellum is shorter than the peduncle. The second segment of the second antennae (pl. 9, fig. 5) has a pair of spines near the apex longer than the ones in the adult (pl. 9, fig. 1). The penultimate segment, instead of the large curved spine near the apex of the inferior margin, bears thereon three pairs of rather long spines and the margin is sinuate. The penultimate segment bears no spines along its margin, and is devoid of the process at its apex. The terminal hooks of the flagellum are much longer and the entire antennae are short and thick.

The second antennae of the supposedly adult male (pl. 9, fig. 4) are about one-third longer than the first pair (pl. 9, fig. 3). The basal segment of the first pair is not very stout, unarmed, scarcely longer than the second; the third segment not half as long as the second; flagellum slightly shorter than the peduncle; the basal segments shorter than those beyond. The second antennae stout; the basal segment with an obscure process or fold beneath; the second unarmed; the penultimate produced into a large slightly recurved spine at the distal end of the lower

margin, not as long nor so stout as in the female, its lower margin continuous in a slightly curved line with that of the segment bearing it; the ultimate segment subcylindrical, slightly arced, a little under one-half of the diameter of the preceding, bearing at its apex an irregular deflected lobe on one side, about one-fifth the length of the first segment of the flagellum and bearing on its lower margin, about one-fifth of its length from the base, a stout spine. Flagellum two-thirds as long as the ultimate segment of the peduncle, first segment four times as long as the second, third segment minute, bearing two claws and numerous setae. A very immature male (pl. 9, fig. 7) besides having the antennae much shorter and thicker, and the second segment of the flagellum not in evidence, shows a distinct tooth at the base, within, of the large curved spine of the penultimate segment of the peduncle, and the apical hooks of the flagellum are longer.

Inner plate of first maxillae nearly obsolete (pl. 9, fig. 9); the outer bearing seven simple spines. The palp 2-segmented; the second segment nearly five times as long as the first, bearing on its apex about 16 spines, the apical spine recurved and serrated. Second maxillae margined with a thick fringe of setae (pl. 9, fig. 8).

First gnathopods with carpus slightly longer and considerably broader than the propodus (pl. 10, fig. 12); ischium with an apical row of long setae; merus with a few setae near the apex; carpus thickly fringed behind with setae a little longer than the dactyl, about eight pairs of setae in front and an oblique row of about six setae near the apex; propodus with six transverse rows of overlapping setae in front, and a few long setae along the posterior margin, oblong, palm slightly receding, emarginate mesally, bearing six marginal spines; dactyl longer than the palm, unarmed, a tuft of setae on the propodus at its base in front.

Second gnathopods (pl. 10, fig. 13) not chelate, with the posterior margin of the merus and anterior of the carpus united throughout their entire length; free margin of merus fringed with two rows of dense setae, about three times the length of the dactyl; front margin of the carpus with a very few long setae;

propodus as long as the merus and carpus united, its apex truncate, an oblique row of long setae on one side, which, being on the reverse side, does not appear in the figure, about six groups of setae on the front margin, four on the posterior, with a short row of long setae at the base; dactyl stout, a little under one-half the length of the propodus, being equal in length to the width of the basal joint, four teeth on its inner margin.

First and second peraeopods similar (pl. 10, fig. 14); basal joint as long as the three following united, half as wide as long, a few short setae on its anterior margin and a number of long setae near the apex of its posterior margin; ischium broader than long, less than one-half the length of the merus; merus large and dilated, one-third longer than the two following segments united, twice the width of the succeeding segments, scattered setae along its margin and a tuft at apex in front; carpus wider than long, wider than the propodus and one-half as long; apex of propodus not wider than the base of the dactyl; dactyl simple, of equal length with the propodus.

Third peraeopod (pl. 10, fig. 15) with the basal joint stout, as long as the two succeeding segments united and two-thirds as broad as long, fringed with a few setae on each margin; ischium broader than long, a few setae on the outer margin; merus nearly one-half longer than the ischium, wider at the apex than base, apex squarely truncate, margins with a few setae; carpus equal in length to the ischium, pear shaped, the base a little more than one-third the width of the apex of the merus, bearing two rows each of about five tooth-like spines, and two or three longer spines at the apex of the hind margin, a tuft of hairs on the front edge; propodus as long as the merus, four times as long as broad, slightly arced, bearing a few small setae and near the apex two small teeth on the hind margin and a bunch of longer setae at the apex of the front margin; dactyl simple, one-half as long as the propodus.

Fourth peraeopod (pl. 10, fig. 16) with the basal joint stout, as long as the three succeeding segments united, about one-half as broad as long, fringed with a few setae on each margin; ischium broader than long, a few setae on the front margin, merus twice as long as the ischium, slightly widened at apex

which is coneaved, margin with a few setae; carpus equal in length to the ischium, irregularly pear-shaped, the base one-third as wide as the apex of the merus, bearing two rows each of about six curved stout spines, the margins with a few setae; propodus as long as the merus, five and one-half times as long as broad, distinctly arced, the hind margin with a few minute setae and two small teeth at apex; dactyl simple, rather stout, scarcely more than a third as long as the propodus.

Fifth peraeopod (pl. 10, fig. 17) nearly twice the length of the third, slender; the basal joint stout, a little longer than the succeeding two united, half as broad as long, fringed on both margins with sparse setae, from half to three-fourths as long as the segment; ischium slightly longer than broad, a few setae on the outer margin; merus more than twice as long as the ischium, one-third as broad as long, not widened at apex, both margins of this and of the succeeding segments armed with groups of long setae; carpus oblong, twice as long as the ischium and more than three times as long as broad, the base about equal to the width of the apex of the merus; propodus one-half longer than the merus, over eight times as long as broad, scarcely arced, with two minute teeth at apex within; dactyl simple, a little more than one-third as long as the propodus.

First uropods (pl. 10, fig. 19) extending beyond the others; rami half the length of the peduncle, the latter fringed on the outer side with setae, a short spine on either side at apex, outer ramus with a long terminal spine, and with its outer edge bearing about twelve spines; inner ramus bearing three terminal spines, its inner edge bearing seven spines. Peduncle of the second uropod twice as broad as long, one-third as long again as its inner ramus; this slender, bearing a long and a short apical spine, and one at the middle of the inner margin; the outer ramus broader, truncate, with a terminal spine, and a few setae along the outer margin. Peduncle of third uropod quadrate, ramus ovate, one and one-half times as long as broad, the margins furnished with long setae.

In alcoholic specimens the ground color is yellow, the antennae and face above marked with brown, and there is a brown band on the base of each dorsal segment.

Length, adult male, 14 mm.; adult female, 9.5 mm.

Type locality, San Francisco Bay.

East Oakland, San Francisco Bay. March 11, 1896; and Alameda Beach, San Francisco Bay, Feb., 1893, collected by Prof. J. S. Holmes. About two dozen specimens, mostly females and some bearing eggs, in the collection of the University of California.

Corophium salmonis Stimpson.

Pls. 11, figs. 20-27; 12, figs. 28-35; 13, figs. 38, 39.

Second antennae of the adult female (pl. 11, fig. 22) about one-third longer than the first (pl. 11, fig. 23). Peduncle of the first pair with the basal segment stout, one-third longer than the second; third segment more than half as long as the second; flagellum about two-thirds as long as the peduncle, the basal segments but slightly shorter than those beyond. Second antennae (pl. 11, fig. 22) stout, the basal segment with the lower margin produced; the second segment bears no spines; penultimate segment subcylindrical, a stout curved spine at the distal end of the lower margin, without teeth above its apex, its lower margin forming a distinct angle with that of the segment bearing it; the ultimate segment cylindrical, one-half as thick as the penultimate, lobed at apex, otherwise unarmed except with bunches of setae; flagellum one-third shorter than the ultimate segment of the peduncle, two segmented, the apical segment bearing two curved terminal spines and numerous setae. In the young females the first antennae have a long spine on the inferior margin of the first joint near the apex; the second antennae bear no spines or processes except the ordinary lobe on the first segment and the apical hooks, they are rather short and tapering; another female evidently somewhat older, bears a pair of spines on the second segment of the second antennae, and one near the base of the inferior margin of the third, another pair in the position of the large curved spine of the adult.

In the full grown male the second antennae (pl. 11, fig. 20) are very long and stout, considerably longer than the entire body, and two and one-half times as long as the first pair (pl. 11, fig.

21). The latter *in situ* reach but little beyond the base of the third segment of the second pair, the basal segment is very much depressed and broadened and bears a long spine near the apex of the middle of the inferior surface; this segment is about one-third longer than the second; the third segment about half as long as the second; flagellum slightly shorter than the peduncle; the basal segments longer than those beyond. The basal segment of the second antennae bears a blunt lobe beneath; the next segment is elongate, one and two-thirds as long as broad, and without spines; three-fourths of the way to the apex along the inferior margin of the third segment, arises a large, stout, curved spine, with a small one of similar shape at its base within; the ultimate segment sub-cylindrical, distinctly arced, with a downward projecting lobe at its apex one one side, and a tooth beyond the first quarter of the inferior margin; flagellum scarcely one-half as long as the ultimate segment of the peduncle; first segment over four times as long as the second; the ultimate segment minute, bearing two small curved spines and a tuft of setae longer than the entire flagellum. What I take to be a very young male (pl. 11, fig. 24) does not differ from the second young female described above; in the male of medium growth, about the size of the adult female described above, the condition is about as there stated, except that the third joint of the second antennae is considerably stouter, and there is a large spine near the base of the fourth.

Inner plate of first maxillae (pl. 11, fig. 25) nearly obsolete, the outer bearing seven spines, three of which are bifid; the palp two segmented; the second segment over four times as long as the first, bearing on its apex seven simple short spines.

Second maxillae margined with setae (pl. 11, fig. 26).

Maxillipedes (pl. 12, fig. 28) with the apical segment of the larger ramus four times as long as broad at base, and much narrowed at base.

First gnathopods (pl. 12, fig. 29) with carpus slightly longer and nearly one-third broader than the propodus; ischium and merus each with a short transverse apical row of long setae; carpus thickly fringed behind with setae considerably longer than the dactyl, a few isolated long setae in front and a short row of

setae at apex; propodus with six or seven transverse rows of overlapping setae, a few scattered setae along the margins, oblong, the palm transverse, convex, unarmed; dactyl longer than the palm, unarmed, a tuft of three setae on the propodus at its base in front.

Second gnathopods (pl. 12, fig. 30) not chelate, with the posterior margin of the merus united to the anterior of the carpus for almost their entire length; free margin of the merus armed with two rows of setae, but little longer than the dactyl; both margins of the carpus with a few long setae at their apices; propodus about one-fourth longer than the merus and carpus united, its apex obtuse, a few scattered setae along the margins, and a tuft at apex, a row of long setae extending from the base obliquely across on one side toward the apex; dactyl slender, its apex much curved, considerably over one-half the length of the propodus, five teeth on its inner margin.

First and second peraeopods similar (pl. 12, fig. 31); basal joint as long as the three following segments united, half as wide as long, bearing a few scattered setae; merus large and dilated, scarcely as long as the two following segments united, twice the width of the succeeding segments, bearing a few scattered setae, and a tuft at the apex in front; carpus scarcely wider than the propodus; apex of propodus obtuse and not wider than the base of the dactyl, which is simple, slender, of equal length with the propodus.

Third peraeopod (pl. 12, fig. 32) with the basal joint not very stout, as long as the three succeeding segments united, and two-thirds as broad as long, with a few setae on each margin; ischium broader than long, a few setae on the front margin; merus more than twice as long as the ischium, scarcely widened at the apex, which is irregularly concave, front margin bearing setae, hind margin with a single medial seta and two at its apex; carpus exceeding the length of the ischium, two-thirds as long as the merus, of irregular shape, its base two-thirds the width of the apex of the merus. It bears two rows each of four or five curved spines, and two longer spines at the apex behind, one or two setae on the front margin; propodus as long as the merus, three times as long as broad, its front margin convex, the hind margin

plane, bearing a small tooth near the apex; dactyl simple, nearly two-thirds as long as the propodus.

Fourth peraeopod (pl. 12, fig. 33) with the basal joint stout, as long as the three succeeding segments united, nearly three-fourths as broad as long, armed with a few long setae; ischium irregularly sub-quadrate, bearing long setae on its front margin; merus about twice as long as the ischium; apex a little widened, slightly concaved, setae on each margin; carpus exceeding the length of the ischium, pear shaped, bearing a tuft of setae at the apex of the outer margin, and two oblique rows of curved teeth, two long teeth at the apex of the hind margin; propodus not quite as long as the merus, arced, scarcely four times as long as broad, bearing two or three setae and a small tooth near the apex; dactyl simple, a little over half the length of the propodus.

Fifth peraeopod (pl. 12, fig. 34) more than twice the length of the third, slender; the basal joint stout, as long as the succeeding two segments united, and two-thirds as broad as long, fringed on both margins with setae from one-half to three-fourths as long as the segment; ischium slightly longer than broad; merus nearly three times as long as the ischium, about one-third as broad as long, not widened at apex, both margins of this and the next segment armed with sparse setae; carpus oblong, more than twice as long as the ischium and over three times as long as broad; the base slightly less than the width of the apex of the merus; propodus one-fourth longer than the merus, slightly bent at base, nearly eight times as long as broad, unarmed except for two small teeth at apex behind and a tuft of bristles at apex in front; dactyl simple, nearly one-half as long as the propodus.

First uropods (pl. 12, fig. 35) extending scarcely beyond the others; rami two-thirds of the length of the peduncle, the latter unarmed; outer ramus with four terminal spines and four spines on the outer margin; inner ramus bearing three terminal spines and four on the inner margin. Peduncle of second uropods not much longer than broad, widened at apex, slightly shorter than its inner ramus; this stout, bearing two or three indistinct terminal spines, and two spines on the inner margin; outer ramus smaller, unarmed except for three terminal spines. Peduncle of the third uropod broader than long, bearing a few setae on each

side, its apex two-thirds wider than the base of its ramus; the latter ovate, slightly constricted at base, not quite two-thirds as broad as long, its margin fringed with long setae.

Color in alcoholic specimens, white or purplish beneath, and a deeper purple above, darker toward the apex of the dorsal segments and on the head. When exposed to strong light the color rapidly disappeared, so that I dare say the specimens in life were much more deeply colored.

Length, adult male, 15 mm.; adult female, 8 mm.

Type locality.—Stomach of salmon from Puget Sound.

The records of the occurrence of the specimens of *C. salmonis* in the collections are as follows:

Karluk Beach, July 23, 1903. Stomach of sockeyes, *Oncorhynchus nerka*, 104-141 mm. long; ten specimens.

Karluk Beach, June 8, 1903. Stomach of young sockeye, *Oncorhynchus nerka*, two specimens.

Karluk Beach, June 8, 1903. Stomach of cohos, *Oncorhynchus kisutch*, eight specimens.

Karluk Estuary, July 24, 1903. Stomach of king salmon (*Oncorhynchus tschawytscha*) fingerlings, 132 mm.; about 100 specimens.

Karluk Estuary, July 24, 1903. Stomach of coho (*Oncorhynchus kisutch*) fingerlings, 71-79 mm.; 150-200 specimens.

Karluk Estuary, July 24, 1903. Stomachs of nine sockeye (*Oncorhynchus nerka*) fingerlings, 102-145 mm.; 200 or 300 specimens.

The specimens of *C. salmonis* were collected in Alaska by the United States Bureau of Fisheries and the data here given concerning this species are published by permission of Hon. Geo. M. Bowers, Commissioner, U. S. Bureau of Fisheries.

Comparison of the Species.

Coloration.—*C. spinicorne* (pl. 13, figs. 36, 37) is distinctly stouter; its ground color is yellow, the antennae and face above are marked with brown, and there is a brown band on the base of each dorsal segment. *C. salmonis* (pl. 13, figs. 38, 39) is more slender, the second antennae of the grown males immensely developed, the color white or purplish beneath, and a deeper purple

above, darker toward the apex of the dorsal segments and on the head. It is thus easy to distinguish the two species by their appearance, although the coloration is not entirely constant.

Antennae.—The spiny armature of the antennae in the different stages varies surprisingly, and might readily prove the source of no little confusion. As a rule in the young and in the females the two pairs of antennae are much more nearly equal in length than in the grown males (compare fig. 39 with fig. 38).

Even very minute females show distinctly a developing egg sac, and very small individuals, with by no means fully developed antennae, sometimes bear egg-masses. I have found females of *salmonis* in several stages, as also of *spinicorne*, and fully developed males of *salmonis*, but of *spinicorne* only stages that possibly do not represent the maximum development of the male. In *salmonis* the second antennae of the males, at least of those fully grown, are very much longer and stouter than those of the female (pl. 13, figs. 38, 39). This is not so noticeably the case in males of *spinicorne*, but may prove to be so if more fully developed males are found (pl. 13, figs. 36, 37).

First Maxillae.—(Pl. 9, fig. 9; pl. 11, fig. 25.) The apical teeth of the palp of the first maxillae of *salmonis* are seven in number and do not form a complete circle; in *spinicorne* they form a complete circle and are about twelve in number, one of the outer ones serrate; on the ramus about three of the teeth are bifid in *salmonis*.

Peraeopods.—(Pl. 10, figs. 14, 17; pl. 12, figs. 31, 34.) The basal segment of the fourth peraeopod is broader in *salmonis*, and the second row of styles on the carpus terminates in two long straight spines.

Uropods.—(Pl. 10, fig. 19; pl. 12, fig. 35.) The first and second uropods show a stout tooth-like process on the apex of the first segment in *salmonis;* both rami of the first uropod have about eight spines, longer and stouter than those of spinicorne, especially than the dozen or so on the outer ramus; the outer ramus of the second uropods has in *salmonis* three long apical styles, and the inner ramus bears about two apical styles and the two large ones along the margin; the basal segment of the third

uropods is larger and the ramus not quite so broad in *salmonis* as in *spinicorne*.

These are the more striking differences. There are many minor differences in almost every appendage.

Zoological Laboratory, University of California,
May 6, 1907.

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EXPLANATION OF THE PLATES.

PLATE 9.

COROPHIUM SPINICORNE Stimpson.

Fig. 1. Second antenna; adult female; × 20.
Fig. 2. First antenna; adult female; × 20.
Fig. 3. Second antenna; adult male; × 20.
Fig. 4. First antenna; adult male; × 20.
Fig. 5. Second antenna; young female; × 20.
Fig. 6. First antenna; young female; × 20.
Fig. 7. Second antenna; young male; × 20.
Fig. 8. Second maxilla; × 53.
Fig. 9. First maxilla; × 53.
Fig. 10. Maxillipede; × 53.
Fig. 11. Mandible; × 53.

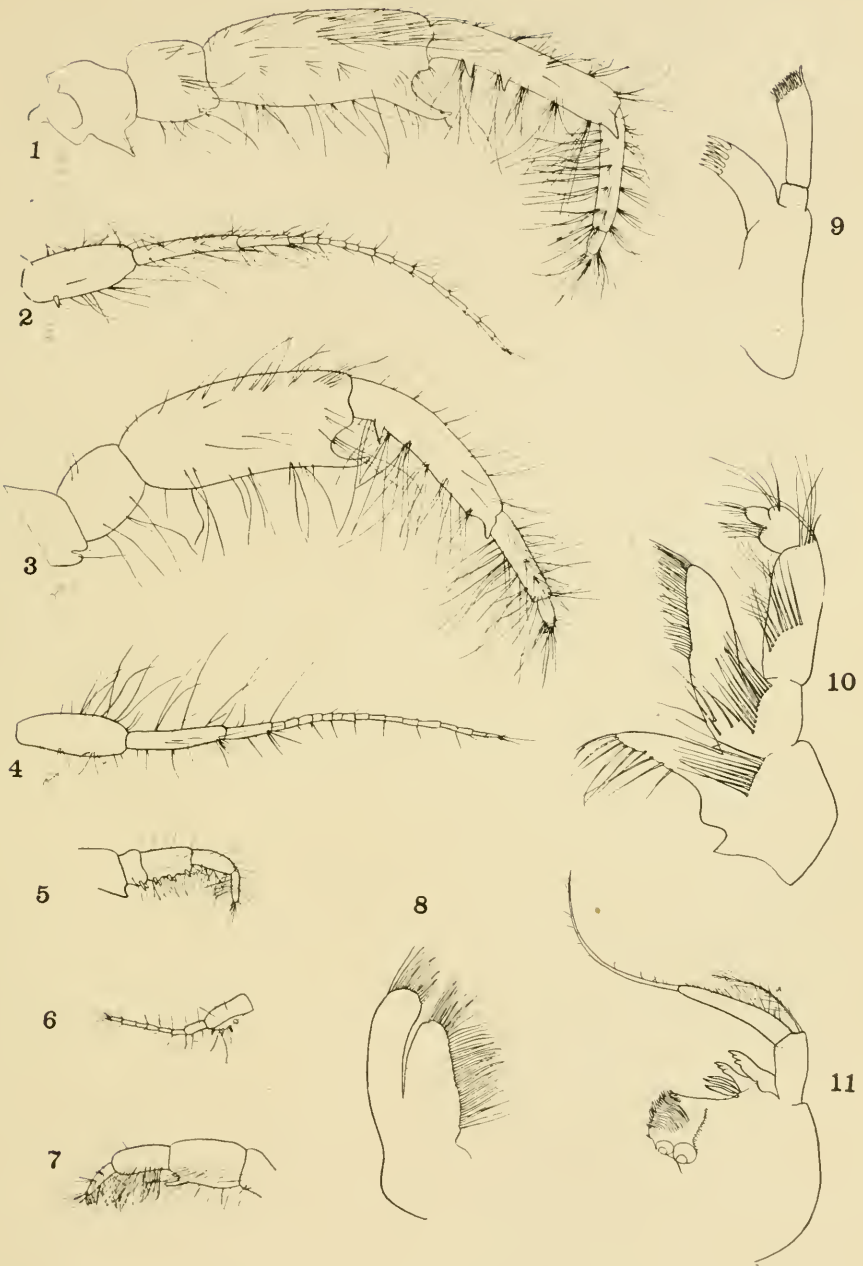
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PLATE 10.

COROPHIUM SPINICORNE Stimpson.

Fig. 12. First gnathopod; × 42.

Fig. 13. Second gnathopod; × 24.

Fig. 14. First peraeopod; × 19.
The second peraeopod is similar to the first.

Fig. 15. Third peraeopod; × 19.

Fig. 16. Fourth peraeopod; × 19.

Fig. 17. Fifth peraeopod; × 19.

Fig. 18. Third pleopod; × 28. The first and second pleopods do not differ from the third, nor from those of *C. salmonis*.

Fig. 19. First, second, and third uropods; × 16.

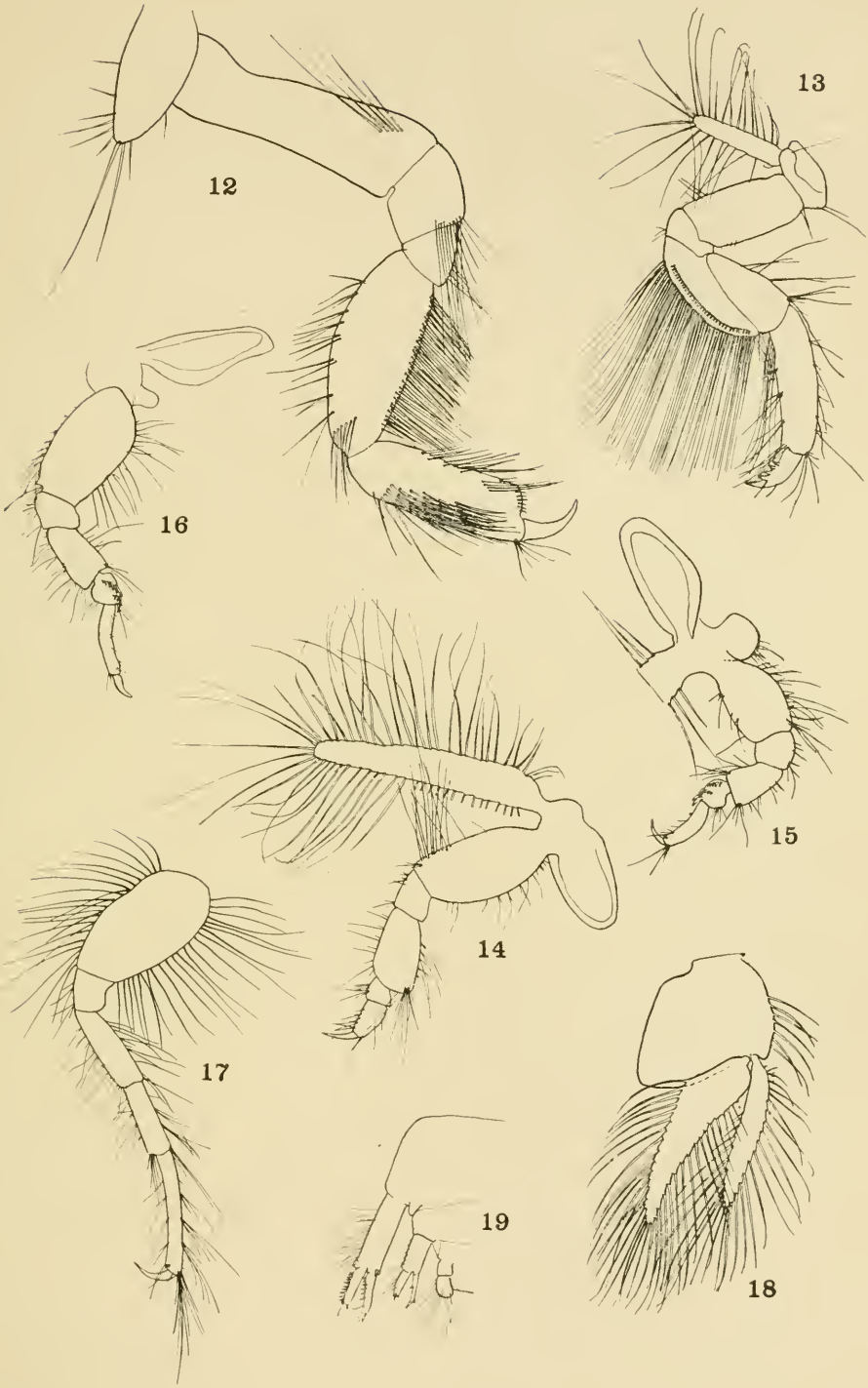
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PLATE 11.

Corophium salmonis Stimpson.

Fig. 20. Second antenna; adult male; × 20.
Fig. 21. First antenna; adult male; ventral aspect; × 20.
Fig. 22. Second antenna; adult female; × 20.
Fig. 23. First antenna; adult female; × 20.
Fig. 24. Second antenna; young male; × 20.
Fig. 25. First maxilla; × 56.
Fig. 26. Second maxilla; × 53.
Fig. 27. Mandible; × 53.

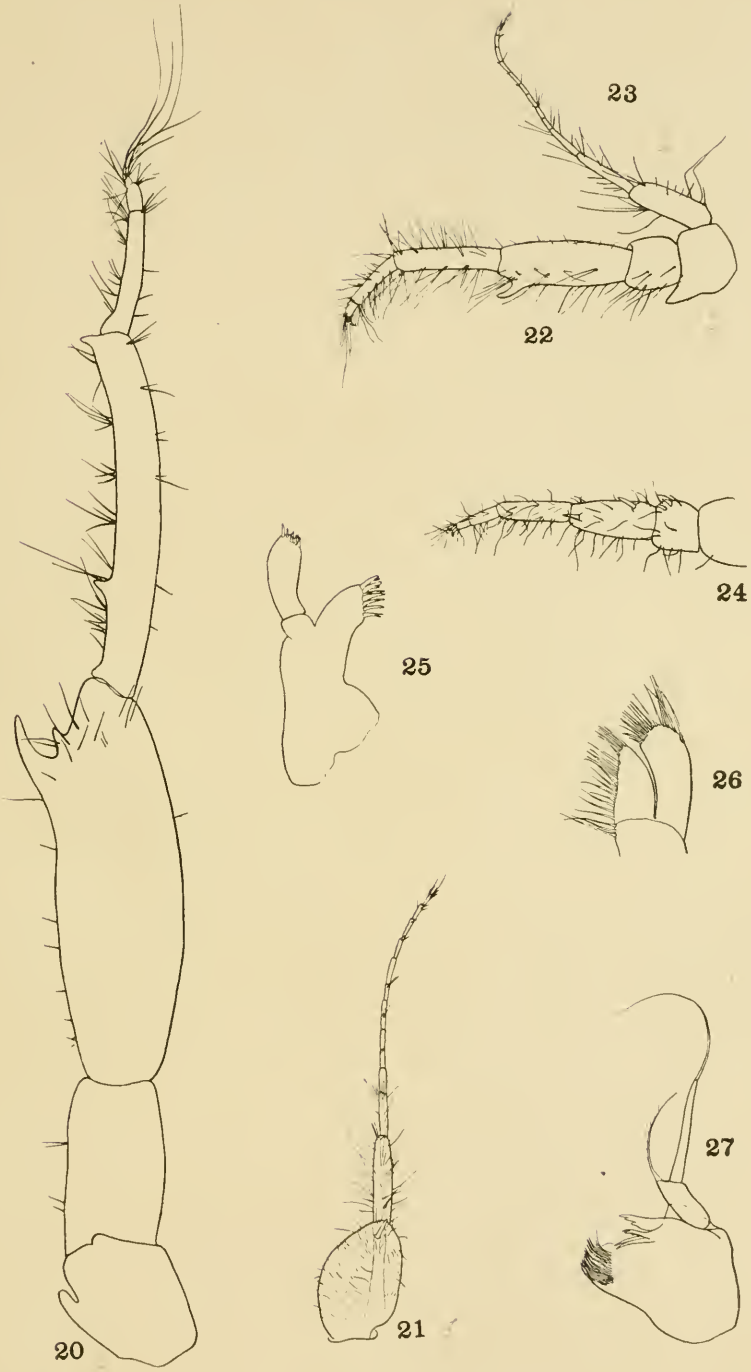
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PLATE 12.

Corophium salmonis Stimpson.

Fig. 28. Maxillipede; × 53.

Fig. 29. First gnathopod; × 44.

Fig. 30. Second gnathopod; × 24.

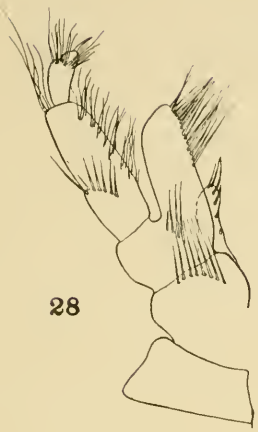
Fig. 31. First peraeopod; × 19.
Second not different from the first peraeopod.

Fig. 32. Third peraeopod; × 19.

Fig. 33. Fourth peraeopod; × 19.

Fig. 34. Fifth peraeopod; × 19.

Fig. 35. First, second, and third uropods; × 16.



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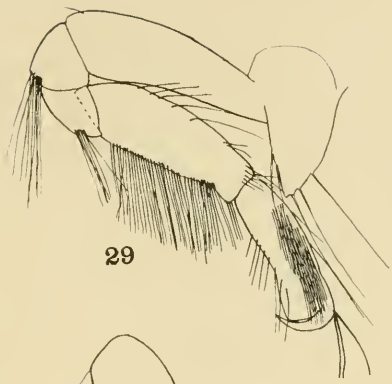

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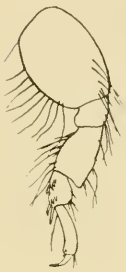

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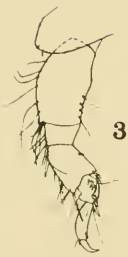

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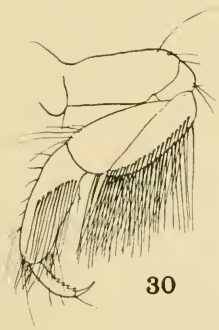

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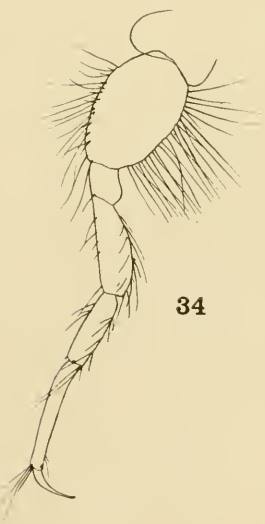

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PLATE 13.

Fig. 36. Adult male of *Corophium spinicorne* Stimpson. × 4.
Fig. 37. Adult female of *Corophium spinicorne* Stimpson. × 4.
Fig. 38. Adult male of *Corophium salmonis* Stimpson. × 4.
Fig. 39. Adult female of *Corophium salmonis* Stimpson. × 4.

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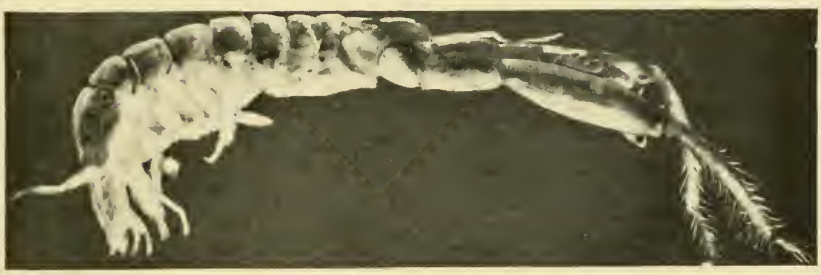

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Vol. 4, No. 5, pp. 253-344, Pls. 14-24 May 27, 1908

CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XX

THE INCRUSTING CHILOSTOMATOUS BRYOZOA OF THE WEST COAST OF NORTH AMERICA

BY

ALICE ROBERTSON

BERKELEY
THE UNIVERSITY PRESS

JUN 25 1908

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XX.

THE INCRUSTING CHILOSTOMATOUS BRYOZOA OF THE WEST COAST OF NORTH AMERICA.

BY
ALICE ROBERTSON.

This paper completes the report on the *Chilostomata* in the present collection of the University of California, and constitutes the second of the series of papers on the bryozoa of the Pacific Coast begun by the writer ('05) in a report on the non-incrusting and flexible Chilostomes of that region. Since no sharp distinction can be made between those Chilostomes which merely incrust, and those which besides may form calcareous, foliaceous colonies, or which grow erect and branching, all the non-flexible Chilostomatous species are included under the present title.

There are included in this report ten families, eighteen genera, forty-five species, and three sub-species. Of these six species and one sub-species are new. New facts are added to our knowledge of many species, more especially of those restricted to this region. Most of these latter were reported by Hincks ('80-'84), frequently from scanty material so that the descriptions were necessarily meager and lacking in details. Of the whole number reported in this paper, nineteen species and one sub-species are restricted to

this coast, the remainder being cosmopolitan or circumpolar. Of the whole number of *Chilostomata* so far reported from our collection, seventy-nine species and four sub-species are recognized. Of these, nineteen species and two sub-species are new, while thirty-eight species and two sub-species are known only from this region. An interesting fact disclosed is the relationship existing between a *cyphonautes,* a larval bryozoan form frequently met with, and *Membranipora villosa,* a species rather abundant on the Pacific Coast.

LIST OF SPECIES TREATED.

Membranipora circumclathrata Hincks.
Membranipora horrida Hincks.
Membranipora lacroixi Audouin.
Membranipora occultata sp. nov.
Membranipora patula Hincks.
Membranipora sandalia Robertson.
Membranipora spinifera Johnston.
Membranipora tehuelcha d'Orbigny.
Membranipora membranacea Linnæus.
Membranipora serrata Hincks.
Membranipora villosa Hincks.
Cyphonautes occidentalis sp. nov.
Micropora coriacea Esper.
Thalamoporella rozieri Audouin.
Cribrilina hippocrepis Hincks.
Microporella californica Busk.
Microporella malusi Audouin.
Lagenipora spinulosa Hincks.
Schizoporella areolata Busk.
Schizoporella auriculata Hassall.
Schizoporella auriculata subsp. *ochracea* Hincks.
Schizoporella biaperta Michelin.
Schizoporella cecili Audouin.
Schizoporella hyalina Linnæus.
Schizoporella insculpta Hincks.
Schizoporella linearis Hassall, subsp. *inarmata* Hincks.
Schizoporella longirostrata Hincks.
Schizoporella oligopus sp. nov.
Schizoporella tumulosa Hincks.
Myriozoum crustaceum Smitt.
Myriozoum coarctatum Sars.
Myriozoum subgracile d'Orbigny.
Hippothoa divaricata Lamouroux.
Lepralia bilabiata Hincks.
Porella concinna Busk.
Escharoides sarsi Smitt.
Smittia trispinosa Johnston.
Smittia californiensis sp. nov.
Smittia collifera sp. nov.
Smittia landsborovi Johnston.
Smittia recticulata J. Macgillivray.
Phylactella collaris Norman.
Mucronella pavonella Alder.
Mucronella californica sp. nov.
Retepora pacifica sp. nov.
Retepora pacifica catalinensis subsp. nov.
Cellepora incrassata Lamarck.
Cellepora costazi Audouin.
Cupularia canariensis Busk.

Phylum Molluscoida Milne-Edwards.

Class **BRYOZOA** Ehrenberg.

Sub-Class **Ectoprocta** Nitsche.

Order GYMNOLÆMATA Allman.

Sub-Order I. Chilostomata Busk.

The first seven families of the Chilostomata, *viz.*, the *Aeteidæ, Eucratiidæ, Cellulariidæ, Bicellariidæ, Notamiidæ, Cellariidæ,* and *Flustridæ,* have been treated by the writer ('05) in a former paper. Of the remaining families, representatives of ten occur on the western coast of North America. All of these are incrusting at some stage of their growth. A few acquire an erect branching habit but are for the most part non-flexible. A strict division cannot be made among the bryozoa, however, on habit of growth, since many species form both incrusting and non-incrusting colonies. One family, the *Steganoporellidæ,* included in those here treated, grows in large incrusting colonies covering the stems and fronds of sea weed, but at any point sending up branches which frequently form tangled masses (pl. 17, fig. 27a). These branches, like those of the *Cellariidæ* which they resemble, are furnished at regular intervals with joints composed of aborted, non-calcified zoœcia which impart to the erect branches more or less flexibility.

It is difficult, indeed impossible, to characterize each family by a word, or in any very easy, simple way. A little experience, however, soon acquaints one with general characters so that there is usually no difficulty in deciding to what family a given specimen may belong. The keys which are here furnished are intended for the use of beginners and are made as simple as possible. They are purely artificial, and apply only to the bryozoa of the California coast. They may or may not apply to foreign species or to new species which may be hereafter described.

KEY TO THE FAMILIES OF INCRUSTING CHILOSTOMATA.

1. Colony circular or oval, convex, probably having power of self movement in the adult stage ..... **Selenariidæ**
1. Colony adherent, immovable 2
2. Margins of zoœcia raised 3
2. Margins of zoœcia not raised 5
3. Front wall depressed, wholly or partly membranous ..... **Membraniporidæ**
3. Front wall depressed, calcareous, on each side below the orifice a thin place in the calcareous wall 4
4. Oœcia bilobate ..... **Steganoporellidæ**
4. Oœcia plain, not bilobate ..... **Microporidæ**
5. Front wall calcareous, traversed by radiating furrows ..... **Cribrilinidæ**
5. Front wall calcareous, not traversed by radiating furrows 6
6. Front wall usually possessing a special pore 7
6. Front wall calcareous not possessing a special pore 8
7. Orifice tubular, pore, when present, circular ..... **Porinidæ**
7. Orifice semicircular, lower margin straight, special pore semicircular ..... **Microporellidæ**
8. Zoœcia acquiring a secondary orifice by growth of peristome 10
8. Zoœcia with simple orifice 9
9. Orifice with sinus on lower margin ..... **Myriozoidæ**
10. Zoœcia urceolate, erect, or suberect, heaped together ..... **Celleporidæ**
10. Zoœcia not urceolate, and not heaped together irregularly 11
11. Zoœcia (a) with large orifice contracted near the lower margin, or, (b) with secondary orifice channelled in front, or, (c) with primary orifice possessing a well developed mucro or tooth ..... **Escharidæ**

Membraniporidae Smitt.

Celleporidæ (part) Johnston, 1847.
Membraniporidæ (part), Busk, 1854.
Flustrellaridæ (part) d'Orbigny, 1850-52.
Flustrellidæ (part) d'Orbigny, *ibid.*
Flustrinidæ (part) d'Orbigny, *ibid.*
Electrinidæ (part), d'Orbigny, *ibid.*
Membraniporidæ Smitt, 1867.
Membraniporidæ, Hincks, 1880.

Zoarium calcareous or membrano-calcareous, incrusting. *Zoœcia* forming a continuous expansion, the front wall more or less membranous.

Membranipora Blainville.

Eschara (part) Pallas, 1766.
Membranipora Blainville, 1834.
Membranipora, Johnston, 1847.
Cellepora d'Orbigny, 1850-52.
Membranipora, Busk, 1854.
Membranipora, Smitt, 1867.
Membranipora, Hincks, 1880.

Zoarium incrusting, sometimes adhering closely to the substratum, sometimes almost free. *Zoœcia* alternate, arranged in linear series and often radiating from a central, primary zoœcium; *margins* raised and more or less calcareous. *Aperture* membranous, depressed, usually occupying the whole of the front of the zoœcium; if occupying but part, the remaining portion covered by a delicate calcareous lamina.

The *Membraniporæ* of the Pacific coast are for the most part incrusting, one species only *M. serrata* Hincks, sometimes forming two-layered foliaceous expansions. An approach to this latter condition is seen in one other species, *M. sandalia* Robertson ('00), which forms a loosely adherent crust. The colonies of this genus, and of many other incrusting genera, originate in a zoœcium of simple form known as the primary *cell* or *zoœcium,* and spoken of by some writers as the *Tata* cell. This is usually entirely membranous and possesses many spines on its margin, often differing widely from the adult zoœcium. Pl. 18, fig. 36 represents the *Tata* stage of *Microporella malusi,* a species somewhat distantly related to *Membranipora.*

The *Chilostomata* and the bryozoa in general, possess a larval stage of greater or less length. The egg develops, sometimes in a special receptacle, the oœcium, sometimes in the zoœcium itself, or perhaps in the water, into a ciliated, swimming larva. Most of these have short existence as free swimming organisms. Many, after a free life of only a few hours or minutes even, settle upon a suitable surface and are quickly transformed into the first or primary zoœcium, the starting point of a colony. The *Membranipora* are interesting as being the only genus among the *Chilostomata* which possesses the remarkable larva known as *Cyphonautes.* This organism is inclosed in a bivalve shell, pos-

sesses a functional digestive tract, locomotor organs, and probably certain organs of sense, and is well fitted to live for a relatively long time in the free swimming stage. A well known *Cyphonautes* of European waters, *Cyphonautes compressus,* metamorphoses into *Membranipora pilosa,* a species not as yet reported from these shores. Certain *Cyphonautes* have been long observed in our waters, however, and recently the metamorphosis of one of them was found to give origin to *Membranipora villosa,* a species restricted to this coast.

KEY TO THE SPECIES OF MEMBRANIPORA.

1. Zoœcia quadrangular, with a spine at each distal angle 2
1. Zoœcia not quadrangular 6
2. Front wall wholly membranous 3
2. Front wall not wholly membranous 8
3. Margins of zoœcia raised, narrow 4
3. Margins of zoœcia not raised, not narrow 7
4. Margins of zoœcia smooth ..... **M. membranacea**
4. Margins of zoœcia more or less serrate 5
5. Front wall beset with minute spines ..... **M. villosa**
5. Front wall not beset with spines ..... **M. serrata**
6. Zoœcia oval, front wall membranous 7
6. Zoœcia not oval 8
7. Margin broad, beset with spines ..... **M. spinifera**
7. Margin broad, without spines ..... **M. lacroixi**
8. Avicularia present 9
8. Avicularia absent 13
9. Aperture occupying only part of the front; beset with spines 10
9. Aperture occupying only part of the front, without spines ..... **M. sandalia**
10. Oœcia immersed, spines few ..... **M. occultata**
10. Oœcia not immersed, spines many 11
11. Aperture broader than long, spines jointed ..... **M. patula**
11. Aperture not broader than long, spines not jointed 12
12. Zoœcia with areolations between them, spines 10-14 ..... **M. circumclathrata**
12. Zoœcia without areolations between them, spines fewer than 10-14 ..... **M. horrida**
13. Zoœcia with thickened calcareous tubercle at each distal angle, tubercles confluent in older parts of colony ..... **M. tehuelcha**

36. **Membranipora circumclathrata** Hincks.

Pl. 14, figs. 1, 2.

Membranipora circumclathrata Hincks, 1881, vol. 8, p. 131, pl. 5, fig. 1.

Zoaria forming small, delicate, spiny, circular incrustations on pebbles or seaweed. *Zoœcia* alternate, elongated, narrowed below and separated from each other by areolations (pl. 14, fig. 1 *are.*); *aperture* oval, occupying at least two-thirds of the front, and closed by a thin membrane; *margin* of aperture narrow, calcareous, raised, slightly crenate on the inner rim; surrounded by a large number of *spines*, some stiff and flaring, others flexible and curving inwards; two, frequently four spines, *fl. sp.*, at the distal margin, stiff, flaring outward and upward; below these, two other stiff spines, *st. sp.*, extending either straight forward or inclining slightly inward; on the lower three-fourths of the aperture, six or eight flexible spines, *sp.*, inclining inward across the aperture and frequently meeting in its middle line. A sessile *avicularium, av.*, just below the margin, calcified lines radiating from it to the edge of the zoœcium forming large, thin walled spaces which with the areolated spaces between the zoœcia characterize this species. *Oœcia* (fig. 2, *œ.*) smooth, with striæ radiating from the proximal or oral margin to the distal margin; a rib extending across the front a slight distance above the oral edge; each oœcium covering the calcified portion of the zoœcium next above having the avicularium, *av.*, of that zoœcium perched apparently upon its summit; these oœcial avicularia usually larger than the ordinary ones on the front of the zoœcia, with tapering mandible extending upward on one side of the aperture; below each oœcium a pair of stiff spines, inclining slightly toward each other.

In his description of this species, Hincks ('81) speaks of finding a line of small holes on the margin of the aperture which he suggests may indicate the position of as many spines. That observer probably possessed only imperfect, mutilated specimens. The colonies here described were in fine growing condition and the margins of the apertures as shown are bordered with spines,

some of which are of great length, the two most distal frequently equaling that of a zoœcium.

This species is reported by Hincks from Santa Cruz, California. Obtained in dredgings from various localities near the coast of southern California.

37. **Membranipora horrida** Hincks.

Pl. 14, fig. 3, 4.

Membranipora horrida Hincks, 1880a, vol. 6, p. 82, pl. 10, fig. 6.
?Membranipora californiensis Waters, 1898, p. 681, pl. 49, fig. 14.

Zoaria forming brittle masses incrusting shells, sponge, and other bryozoa. *Zoœcia* ovate, more or less distant, alternate (pl. 14, fig. 3); *aperture*, sometimes oval, sometimes almost circular, and closed by a membranous wall; *margin* raised, thickened, and slightly crenate; on young zoœcia, or on those in protected portions of the colony, four or six long, stout *spines* on the upper half of the margin; on the lower half and springing from the outer edge are frequently four, but sometimes six delicate spines overlapping the front wall but not meeting. Immediately below the aperture and somewhat to one side of the median line, is a slightly elevated *avicularium* with long tapering mandible directed obliquely either toward the right or left, sometimes curving slightly around the margin of the aperture; sometimes a second smaller *avicularium* appears below the aperture with mandible pointing in a direction opposite to that of the other. Occasionally a few very large *avicularia* are found (fig. 4) which in size are equal to about half that of an ordinary zoœcium, the lower portion, *zoe.*, representing the part of the zoœcium occupied by the polypide, the upper portion, *op.*, representing the operculum and forming the mandible of the avicularium, the whole surrounded by a calcareous margin similar to that surrounding the zoœcia; mandible broad and rounded at the tip; directed distally. *Oœcia* (fig. 3, *oe.*) small, rounded, smooth, a rib across the front a little above the oral rim; sub-immersed, the avicularium which is ordinarily below the aperture resting partly upon the oœcium.

Much variation, especially in the number of the spines and in

the number and size of the avicularia, occurs in the specimens from different localities, as also in various portions of the same colony. The number of spines as given in the diagnosis and as shown in fig. 3 is found only in the younger zoœcia, or upon those in protected positions and without ovicells. The delicate spines on the lower half of the zoœcium are exceedingly variable, four being the commonest number, though sometimes there are only three, and again there may be six. But few of the large avicularia (fig. 4), which are merely transformed zoœcia, have been found and those on colonies from northern California.

Comparison of the various specimens in this collection with *M. horrida* Hincks, and *M. californiensis* Waters, leads me to suspect that these are one and the same species and identical with the form here described. Certainly the resemblances between oœcia and avicularia are striking and most of the differences can be accounted for either by imperfect description due to a lack of material or to variation due to differences in environment.

Membranipora horrida is reported by Hincks from California. It is present in our collection from Puget Sound, Washington; also from various localities on the northern coast of California, Pacific Grove being the most southern point from which it has been obtained. *M. californiensis* is reported by Waters from California.

38. **Membranipora lacroixi** (Audouin) Hincks.

Pl. 14, fig. 5.

Flustra Lacroixii (Audouin) Savigny, 1811, pl. 10, fig. 9.
Flustra distans Hassall, 1841, vol. 7, p. 369.
Membranipora Lacroixii, Busk, 1854, pt. 2, p. 60, pl. 69, figs. 1, 2, 3, 4, 5.
Biflustra Lacroixii, Smitt, 1873, pt. 2, p. 18, pl. 4, figs. 85-88.
Membranipora Lacroixii, Hincks, 1880, p. 129, pl. 17, figs. 5-8.
Membranipora Lacroixii, Waters, 1898, p. 679, pl. 48, figs. 14, 15.
Membranipora Lacroixii, Robertson, 1900, p. 323.

Zoarium forming a dark reticulated incrustation over shells or other bryozoa. *Zoœcia* oval, somewhat elongated, *aperture* occupying the whole of the front; *margin* thickened, rounded, granulated, sometimes forming a prominent ridge, sometimes

rather narrow (pl. 14, fig. 5). In the matrix in which the zoœcia are imbedded, two triangular hollow spaces, *tri. spa.,* just below the aperture of each zoœcium. *Oœcia* none.

This species is quite abundant on our southern coast, having been obtained at various points near San Pedro and San Diego, California. Also found less abundantly at Kadiak, and Orca, Prince Williams Sound, Alaska.

39. **Membranipora occultata** sp. nov.

Pl. 14, figs. 6, 7, 8, 9.

Membranipora unicornis, Robertson, 1900, p. 324.

Zoarium incrusting, forming a somewhat delicate lace work closely adhering to the substratum. *Zoœcia* alternate, elongated; *aperture* oval, occupying from two-thirds to three-fourths of the front; *operculum* rather broad, not semi-circular; *margin* raised, calcareous, slightly crenate on the inner edge; on each side of the lower half of the aperture a *spine,* sometimes stiff (pl. 14, fig. 6, *st. sp.*) and outstanding, sometimes flexible (fig. 7, *fl. sp.*) and inclined over the aperture; often but one spine (fig. 6) which is then usually stiff and projecting outward; on the lower third or fourth of the zoœcial wall just below the aperture, an *avicularium* (figs. 6 or 7 *av.*) with elongated beak, its tip much raised and directed obliquely upward, or infrequently downward; scattered irregularly through the zoarium a few spatulate *avicularia* (fig. 8) with rounded mandible directed upward. *Oœcia* (fig. 7, *oe.*) small, membranous, or very slightly calcareous; almost completely covered, as by a hood, with the calcareous wall (fig. 9, *cal. wa.*) of the lower part of the distal zoœcium, behind which the oœcium, *oe.,* is hidden; the wall, *cal. wa.,* not uniting with the proximal edge of the oœcial wall but standing out leaving a considerable space between it and the oœcial wall; surmounted by an avicularium, *av.,* with long tapering mandible whose tip is raised and frequently covering the lower rim of the aperture of the distal zoœcium.

The most characteristic mark of this species is the submersion of the oœcium under the wall of the distal zoœcium, which thus hides it more or less completely as behind a stiffened veil. The

line made by the lower rim of the encroaching wall has the appearance of a rib across the front of the oœcium for which it was previously taken. This species resembles *M. unicornis* in several particulars, and was formerly so identified. Doubt was always felt, however, concerning the former identification, since the number and position of the spines, the size of the avicularia, and the direction in which the mandible points were different from that given for *M. unicornis* from other localities. These differences were considered of minor importance since they occurred in elements of the colony which are extremely variable. Now, however, taken in connection with the hooded ovicell they neeessitate the formation of a new species.

Membranipora occultata has been found at Yakutat and Juneau, Alaska, in both eases incrusting a tunicate.

40. **Membranipora patula** Hincks.

Pl. 15, fig. 10.

Membranipora patula Hincks, 1881, vol. 7, p. 150, pl. 9, fig. 4.
Membranipora patula Hincks, 1882, vol. 10, p. 465.

Zoaria forming brown or reddish brown patches on rock, pebbles etc. *Zoœcia* large, short and broad, distal extremity much raised; *aperture* occupying from two-thirds to three-fourths of the front wall, usually broader than long, arched above, lower rim curving outwardly; the lower portion of the front of the zoœcium covered by a delicate calcareous lamina which is often continued up the side and around the top of the aperture (pl. 15, fig. 10). Four, five, and sometimes six long, cylindrical, jointed *spines* on the upper margin, *sp.* From the back of the zoœcium and arising some distance below the distal margin, an *avicularium*, *av.*, which viewed from the top is triangular in shape with mandible directed distally, or toward the growing rim of the colony; frequently absent. Oœcia, *oe.*, shallow, smooth, scattered, apparently immersed in a forest of spines.

Membranipora patula is reported by Hincks from California, and in large quantity and of luxuriant growth from Queen Charlotte Islands. Small colonies have been obtained at several southern localities at depths varying from 15 to 42 fathoms.

41. **Membranipora sandalia** Robertson.

Pl. 15, figs. 11, 12, 13, 14.

Membranipora sandalia Robertson, 1900, p. 324, pl. 20, figs. 9, 9a, 9b; pl. 21, fig. 10.

Zoarium adherent, though rather loosely attached to the substratum, delicate, brittle; spreading out in a fan-shaped expansion, the gelatinous margins often convoluted, and apposed surfaces often growing together, forming ridges over the colony. *Zoœcia*, in younger stages oblong, quadrangular, *aperture* occupying the whole of the front (pl. 15, fig. 11); in older stages calcareous ribs extending from the median line to the margin of the lower two-thirds or three-fourths of the zoœcial wall (fig. 13) this portion finally becoming covered by a delicate calcareous crust (fig. 14). *Aperture*, in adult stage (fig. 14, *ap.*), occupying about one-third or one-half of the front wall. An *avicularium*, *av.*, with pointed mandible directed right or left on the lower margin of the aperture. *Oœcia?*

Membranipora sandalia illustrates well the changes that often take place from the early stages of zoœcial growth to the adult stage. The zoœcia on the margin of a colony possess a membranous aperture (fig. 11, *ap.*) that fills the whole space between the calcareous margins; at a slightly later stage, calcareous denticles (fig. 12, *d.*) appear on the lateral margins of the lower portion of the zoœcium and the future aperture, *ap.*, is outlined by a circular rib whose extremities do not quite meet in the median line. At a still later stage (fig. 13) the denticles have grown out forming ribs, *rb.*, extending toward the base of the aperture or toward a median line dividing the basal portion of the zoœcial wall into large areolations. The ribs stop rather abruptly at an area, *ar.*, below the aperture on which there forms, in the adult stage (fig. 14), a large, sessile avicularium, while the ribs on the lower portion of the zoœcium are almost or completely hidden by a delicate calcareous lamina. In the stage represented by fig. 14, the general aspect of the zoœcia is so different from that of those on the margin of the colony, that they might seem to belong to different species were the transition stages of growth not found.

Membranipora sandalia has been obtained at Yakutat, Alaska, growing over sponge.

42. **Membranipora spinifera** (Johnston) Alder.

Pl. 15, fig. 15.

Flustra spinifera Johnston, 1838, vol. 2, p. 266, pl. 9, fig. 6.
Flustra lineata, (part) Johnston, 1847, p. 349.
Membranipora spinifera, Alder, 1857, p. 247.
Membranipora cymbæformis Hincks, 1877, vol. 19, p. 99.
Membranipora spinifera, Hincks, 1880, p. 149, pl. 19, figs. 1, a, b, c.

Zoaria forming large brown patches on rocks, pebbles, etc. *Zoœcia* elongated, oval, alternate (pl. 15, fig. 15); *margin* rather wide, raised, calcareous, roughened with minute papillæ; with a variable number of *spines*, 10, 12, or more; two at the summit of the zoœcium, very long and flaring outward and upward; a second pair, very stout and directed outward; the remainder more slender and bending inward, almost meeting over the aperture; *aperture* occupying the whole of the front. *Avicularium* elongated, articulated to the side of the zoœcium about the middle, or just above it; erect upon a pedicel almost as long as the second pair of spines; mandible acute and directed outward. *Oœcia* shallow, smooth, with a rib across the front.

This species has been found at Orca, Prince Williams Sound, Alaska; found also in considerable abundance on the rocks and seaweed at various points on the California coast.

43. **Membranipora tehuelcha** (d'Orbigny) Waters.

Pl. 15, figs. 16, 17; pl. 16, fig. 18.

Flustra tehuelcha d'Orbigny, 1839-46, vol. 5, pt. 4, p. 17, pl. 8, figs. 10-14.
Biflustra tehuelcha d'Orbigny, 1850-52, p. 328.
Membranipora tuberculata Busk, 1859, p. 30, pl. 2, fig. 1.
Biflustra denticulata, Smitt, 1873, pt. 2, p. 18, figs. 89-91.
?Amphiblustrum bituberculatum Ortmann, 1890, p. 29, pl.1, fig. 25.
Membranipora tehuelcha Waters, 1898, p. 674, pl. 48, figs. 6-8.

Zoarium incrusting stems and fronds of fucus with a white calcareous incrustation covered with tubercles. *Zoœcia* (pl. 16, fig. 18), elongated, alternate; *aperture* occupying about two-thirds of the front, depressed, surrounded by a calcareous border on whose inner rim are four, five, or six short denticles or teeth. Below the aperture, two thick, blunt, calcareous *spines, sp.,* or

tubercles which frequently coalesce, forming a broad calcareous plate projecting above each zoœcium; the aperture then seeming to be guarded above and below, and flanked on each side by a pair of projecting processes. *Oœcia* not known.

This species is very characteristic and may be readily identified by its white calcareous incrustation investing the stems of the common rockweed. The diagnosis given applies to the older stages only. In different parts of the colony the zoœcia present very different appearances. The growing rim (pl. 15, fig. 16, *gr. r.*) consists of a gelatinous mass divided by longitudinal lines marking the lateral boundaries of the zoœcia, each division containing an apparently undifferentiated mass of cells, *cl. m.* Lines at right angles to the lateral walls soon appear some distance below the growing rim, marking off that portion into quadrangular spaces and forming the proximal and distal walls of the future zoœcia. The lateral walls at the same time become distinctly raised, and from their inner margin there grow at irregular intervals, numerous irregularly shaped spinous processes, *sp. pro.,* some forked, others meeting across the intervening space. At this stage, the aperture occupies the whole of the front, and except for the irregular processes projecting from the walls, the zoœcia have an appearance much resembling *M. membranacea;* neither polypide nor operculum is yet formed, but in the interior the mass of protoplasm, *pro. m.,* destined to form the polypide may be seen, and in the young zoœcia below, the polypides, *pd.,* are found in various stages of development. At a slightly later stage of growth (fig. 17) the lateral margins of the zoœcia become raised and the proximal and distal margins adjoining each other become covered by a calcareous wall, *cal. wa.;* the outer distal angles, *ang.,* of each zoœcium become much thickened and show a tendency to project; the aperture acquires a semi-circular operculum consisting of a bar of chitin, and the polypide is formed. In retraction, *re. pd.,* this is drawn into the proximal portion of the zoœcium behind the calcareous wall. In the older parts of the colony the calcareous deposition increases greatly reducing the size of the aperture (pl. 16, fig. 18, *ap.*); the distal angles thicken and project in two blunt processes or spines, *sp.,* which sometimes coalesce into a single bifid tubercle, or even into

a single broad calcareous plate. In this stage the margin of the aperture becomes thicker and acquires from four to six short spines directed inward.

The various stages of growth of this species are thus seen to be extremely diverse and well marked. Whether or not the various synonymes refer to the same species is difficult to say without a knowledge of these stages of growth. D'Orbigny ('39-'46) first described *M. tehuelcha* from Patagonia and reports it as abundant on the east coast of South America from Pernambuco southward. Waters ('98) suggests that *M. hyadesi* Jullien, from Cape Horn, may be the same thing or a variety. This may be so, although the size and the relatively slight amount of calcareous deposit would seem to separate *M. hyadesi* from *M. tehuelcha* unless Jullien has figured an immature specimen. *M. hyadesi* is, perhaps, more closely related, as I will show, to *M. serrata* Hincks of the California coast. The present species seem to be closely related to, if not identical with, *Amphiblustrum bituberculatum* Ortmann, both having the blunt, calcareous tubercles and the aperture much reduced by the growth of the calcareous deposit around it.

Membranipora tehuelcha is obtained from San Francisco southward on our coast. It is one of the most abundant species on the rock-weed at La Jolla, San Diego, and San Pedro.

44. **Membranipora membranacea** (Linnæus) Blainville.

Pl. 16, figs. 19, 19a, 20.

Flustra membranacea Linnæus, 1766-68, p. 1301.
Flustra membranacea, Ellis and Solander, 1786, p. 18.
Membranipora membranacea, Blainville, 1834, p. 447.
Flustra membranacea, Johnston, 1847, ed. 2, p. 348, pl. 66, figs. 1, 2, 3.
Reptoflustra telacea, d'Orbigny, 1850-52, p. 324.
Membranipora membranacea, Busk, 1854, pt. 2, p. 56, pl. 1.
Membranipora membranacea, Hincks, 1880, p. 140, pl. 18, figs. 5, 6; pl. 68, fig. 2.

Zoaria consisting of circular patches from two to five or six centimeters in diameter incrusting stems and fronds of *fucus*. *Zoœcia* quadrangular, oblong, alternate (pl. 16, fig. 19) arranged in lines radiating from a center (fig. 20); *margins* slightly raised;

aperture occupying the whole of the front, closed by a transparent, rather delicate membrane; at each anterior angle a blunt chitinous *spine; operculum* a simple, curved, semi-circular bar of chitin (fig. 19a). *Oœcia* wanting.

This species is found only in moderate quantity on the shores of Alaska, Puget Sound, and California. It is not so abundant in the dredgings as the next species described, *M. serrata* Hincks, nor have I ever found it on the shore seaweed in anything like the quantity in which that species is commonly obtained. Until one has acquired experience there is no difference discernible to the naked eye between these two species and the same habit sketch (fig. 20) answers for both.

45. **Membranipora serrata** Hincks.

Pl. 16, figs. 20, 21, 21a.

Membranipora membranacea form *serrata* Hincks, 1882, p. 469.

Zoaria consisting of circular patches incrusting seaweed (pl. 16, fig. 20), especially the fronds of the giant *fucus* of this coast; colonies frequently numerous and by their coalescence covering the entire surface on which they are growing. *Zoœcia* quadrangular, oblong, alternate, arranged in lines radiating from the center of the colony (fig. 20); *aperture* occupying the whole of the front, closed by a membranous front wall; *margins* raised, with a calcareous, crenated, inner rim, some of the crenations growing long and forming distinct denticles; usually a rather long *denticle, d.,* in the middle of the proximal rim of each zoœcium, and often several at irregular intervals on the lateral margins; *operculum* (fig. 21a) curved, its margin strengthened by a chitinous rib, the proximal ends of which are drawn toward each other so that a line joining them is shorter than one cutting the rim of the operculum above its proximal extremities, *i.e.,* the curve of the operculum is greater than a half circle. At each distal angle a short *spine*. *Avicularia* and *oœcia* wanting.

Hincks gave but a short description of this species without figure, considering it a form of *M. membranacea*. From the examination of a large quantity of material from various localities it seems justifiable to consider this a distinct species. The ser-

rated border is always present, and is even found in young zoœcia near the outer growing margin of the colony. This is never true of *M. membranacea* of this locality and transition stages have not been observed. The operecula of the two species differ in shape, that of *M. serrata* being deeper and narrower than that of *M. membranacea*. There is considerable resemblance between this species and *M. hyadesi* Jullien ('88). Both have the crenulated border well developed, with the membranous aperture, but the spines of our species are not elevated upon a calcareous tubercle as are those of the Patagonian form.

Hincks reports this species from Queen Charlotte Islands. It has been obtained in great abundance in Puget Sound, and has been dredged and collected between tide marks on the shores of southern California. At Monterey, California, it occurs in free, very much folded and contorted, foliaceous masses.

46. **Membranipora villosa** Hincks.

Pl. 16, figs. 22, 22a, 22b, 23; pl. 17, figs. 24a, 24b, 25.

Membranipora villosa Hincks, 1880a, vol. 6, p. 84, pl. 10, fig. 8.
?Flustra Isabelliana d'Orbigny, 1839-1846, vol. 5, pt. 4, p. 18, pl. 8, figs. 20-24.

Zoaria forming somewhat delicate incrustations on the stems, fronds, and floats of kelp. Colonies circular, the lines of zoœcia radiating from the point of origin near the center. By the coalescence of a large number of colonies the entire surface of frond or float of seaweed is often covered. The first zoœcia formed and those constituting the first few rows near the center of a colony differ markedly in size and ornamentation from those which form the outer rows and larger part of a colony. These latter are most often seen in general collections and are apparently the type described by Hincks ('80a). The description here given embraces both early and later stages of growth, but for convenience because the later stage of colonial formation is more often met with, it is first described.

Zoœcia quadrangular, elongated (fig. 22); *margins* thin, with a calcareous, slightly crenate inner rim; *aperture* occupying the whole of the front and covered by an exceedingly transparent,

membranous front wall; *operculum,* when closed, apparently of the *membranaceous* type, *i.e.,* consisting of a semi-circular chitinous rod (fig. 22a); when partly open (fig. 22b) the rod is seen to be widened at the proximal extremities affording a wide base for the attachment of the opercular muscles, *mus. att. Spines* are of three kinds on each zoœcium: a stiff, curved, flaring spine (fig. 22, *fl. sp.*) at each upper or distal angle; on the lateral margins, at irregular intervals, one, two, or more flat spines, *lat. sp.,* flaring outward; springing from the wall of the aperture, extending from the lower end of the operculum around the zoœcium, a short distance within the crenate margin, a row of 15 or 20 minute frontal spines, *fr. sp.,* whose points are directed toward the median line. Occasionally, at the middle of the upper margin of some zoœcia, a tall hollow spine, *t. sp.* These tall processes are probably of a different nature from the ordinary bryozoan spine. They usually occur at a point where two lines of zoœcia either converge or diverge, and are most abundant on colonies spreading over an uneven surface. At the points where zoœcia converge, *e.g.,* triangular or circular spaces are frequently formed within some of which a polypide may sometimes be found, and at the angles or irregularly around the margin of such spaces extra large spines frequently occur; at other times, instead of a zoœcium, a tall spine-like process develops, *t. sp.,* this process being probably homologous with the zoœcium and contained polypide which should otherwise have developed at that point of the colony.

A young colony consisting of only seven zoœcia is shown in fig. 23. The *zoœcia* are oval in the earliest stage, becoming somewhat elongated in the second and third rows; *margin* thin, rounded above, raised, without the crenate, calcareous, inner rim; *aperture* occupying the whole of the front, covered by an exceedingly delicate membranous front wall; margin surrounded by *spines* of great length which are frequently much branched, *br. sp.* On the third zoœcium, *c.*, minute frontal spines occur on the membranous front wall at more or less regular intervals inside the margin, and these structures are found on all future zoœcia of the colony, while the branched marginal spines disappear.

This earlier stage of colonial formation has not been hitherto described and the appearance of the zoœcia in the two stages of growth is so different that it is difficult to believe them stages of one and the same species unless the transition steps are seen. Many colonies showing these transitions were obtained at La Jolla during July of 1905. At that time of year the larvæ are settling, and new, fresh colonies are abundant. The youthful condition with branched spines (fig. 23) continues for about ten or twenty rows when the adult stage (fig. 22) with elongated zoœcia and unbranched spines is assumed.[1]

Membranipora villosa is found at various localities from Puget Sound to San Diego, and is probably very abundant in the belt of kelp some distance out from shore on our southern coast.

This species is especially interesting from the fact that it is one of the few members of the genus Membranipora whose metamorphosis from a *Cyphonautes* larva has been observed. Cyphonautes was originally described by Ehrenberg ('33) as a rotifer, and was re-described by Johannes Muller ('54) as a larva of an annelid. Later, in 1857, Semper declared his belief in its mollusean affinity, and it was not until Schneider in 1869 watched its metamorphosis, that the true relationship of this interesting organism became known. Schneider found it extremely difficult to keep *Cyphonautes* under artificial conditions. Indeed, he found it impossible to do so unless the larvæ were matured at the time of capture and just about to settle. It was by a rare piece of good fortune that the relation between the *Cyphonautes* common on the Pacific coast and its sessile form was discovered. On a kelp brought into the laboratory at La Jolla during the summer of '05, were found multitudes of minutes bodies covering every portion

[1] Since writing the above, I have had the opportunity to examine figures of d'Orbigny's *Flustra Isabelliana*, and consider the resemblance between it and the adult stage of *M. villosa* Hincks as most striking. There is a possibility that the two species are identical, in which case d'Orbigny's name should have the preference. *Flustra Isabelliana* is evidently a *Membranipora* and like *M. villosa*, has spines at the anterior margin and has its front wall ornamented by two rows of minute spinules (petites pilosities). In view of the full description of the stages of growth of *M. villosa* here given, and until more knowledge can be obtained of the development of *F. Isabelliana*, or until direct comparison of *M. villosa* with the South American species can be made, it is not considered best to do more at this time than to call attention to the similarity and possible identity of the two species.

of the plant. On inspection, these were found to be bryozoan colonies consisting in many instances of two, three, five, or more zoœcia. Toward the extremities of the fronds larger colonies were found numbering sometimes hundreds of individuals, and all were identified as colonies of *M. villosa.* Further examination showed the larva in every stage of metamorphosis, from the earliest in which the shell (fig. 24a) is still fastened to the surface upon which it settles, to the latest in which zoœcia were formed and polypides were functioning.

The metamorphosis of at least two other Membraniporæ has been observed (Ostroumoff '85), and according to Kupelwieser ('06) who has recently studied *Cyphonautes* from many localities, these organisms are to be distinguished mainly in size and in the denticulation of the shell. The drawing here given of our western *Cyphonautes* (pl. 17, fig. 24) was made from life, as were also the observations recorded. They will acquaint the student with the main facts of structure and habits, but for more exhaustive treatment he is referred to the literature cited in the bibliography. For the sake of differentiating this western form from other *Cyphonautes* it will be referred to as *C. occidentalis.*

Like the familiarly known *Cyphonautes compressus*, *Cyphonautes occidentalis* (pl. 17, fig. 24) is triangular in shape and is inclosed in a delicate bivalve shell. The proportion of height to greatest breadth is on an average as 5:7. For purposes of orientation, the wide ciliated border is known as the oral, *o.*, side, the apex of the triangle, the aboral, *ab.*; the side parallel with the intestine is posterior, *post.*, and the side opposite is anterior, *ant.* On the oral side the valves of the shell gape, permitting free communication between the exterior and the interior. The oral edges are thickened with a wide chitinous border, and still further strengthened by a reddish brown chitinous rib, *rb.* This rib is beset with a number of strong red, denticles, *d.*, or teeth which are numerous at the angles of the shell, being there set in two or more alternating rows, while in the intermediate region they form a single row. The apex, *a.*, of the shell is deeply cut on the two valves, and through the opening the apical tuft, *ap. t.*, of cilia protrudes. The animal within the shell differs but little from *C. compressus.* From observation of the living organism only,

there seem to be two rings of cilia at the oral rim, unconnected in the middle. The interior cavity is divided into three parts: a median part or atrium leading directly to the mouth, *m.*; an anterior atrium whose rim is surrounded by the anterior ring of cilia and which contains the pyriform, *pyr.*, body; and a posterior atrium into which the digestive tract opens, *int.* The median atrium, known as the oral atrium, is deep and lined on all sides with cilia which lash upward. Currents containing food particles are thus set in motion toward the mouth, *m.*, which opens directly into a large stomach, *stm.*, and this into the intestine, *int.* In the intestinal atrium is a large gland-like body, *suc.*, which Ostroumoff ('85) first pointed out is the disk or sucker so-called by which fixation of the larva takes place. Beside the sucker is the adductor muscle, *add.*, of the shell. The tuft of cilia at the apex extends from a cell plate known as the retractile disk, *re. d.* Between it and the pyriform body there extends a bundle of fibers, *fi.*, in which movements of contraction are frequently visible. Protruding from the antero-oral rim, below the pyriform body is a tuft of long stiff cilia, *st. c.*, whose movements are synchronous with the movements in the fibers connecting the retractile disk and the pyriform body. Prouho ('90) in investigating a similar fibrous strand in the larva of *Flustrella*, a larval form very similar to *Cyphonautes*, ascribes to the fibers connecting the retractile disk and the pyriform body both a contractile and a nervous function, considering that the fibers are of two kinds, muscle fibers and nerve fibers. According to Kupelwieser ('06) not only does this bundle of nervo-muscular fibers connect the retractile disk and the pyriform body, but a functional relation exists between the tuft of stiff cilia, *st. c.*, and this fibrous strand. The tuft of stiff cilia, this investigator considers, exercises an important sensory function in the discrimination of food particles, and a mechanical function in getting these particles into the food current passing into the median atrium and thus into the mouth. The bundle of mixed fibers partly effect, partly regulate the movements of the stiff cilia in the performance of these functions.

In swimming, Cyphonautes moves in circles, generally tilted so that the aboral side is forward, and half of the shell and con-

sequently the organs of one side of the animal are visible. When moving very rapidly it often stands upright with the aboral end directed upward or sometimes downward. As conditions become more unfavorable, movement of translation ceases, and the animal lies on its side, remaining for some time in an uncontracted state, that is, the atrial cavities remain open; as conditions become still more unfavorable, quivering motions are set up in the bundle of fibers extending between the pyriform organ and the retractile disk, and finally the whole body contracts into a mass in which both organs and atria are indistinguishable.

Examination of the kelp containing young stages of colony formation of *M. villosa* soon revealed many instances of the fixation of the larva. In the earliest stage observed (pl. 17, fig. 24a) the shell is seen to have opened along its anterior edge and to have flattened over its contents, its edges being closely applied to the surface of the kelp and the shell being slightly raised in the middle. At first the larval organs form an indiscriminate mass, apparently undifferentiated, retaining the shape of the flattened shell, but smaller than it. In the cellular mass, lines of differentiation soon appear, and a border forms inclosing two cell masses, *a* and *b*, and between them a third, *c* (fig. 24a). The interior is thus divided into three distinct masses of cells and into two chambers, *a* and *b*, which constitute the first two zoœcia of the new colony. The masses of cells in fig. 24a become transformed into the first two polypides, *a'* and *b'* (fig. 24b). On the border of the young zoœcia four or five long bifid spines extend outward while on the wall of the aperture just below the operculum, one or two minute frontal spinules, become visible. The twin polypides seem to advance with equal rates of growth. Between the apices of the zoœcia the cell mass, *c*, becomes the fundament of the third zoœcium (fig. 25) with its polypide. On each side of the third zoœcium another forms, all being furnished with extremely long branched spines, the marginal zoœcia having four or five, the intermediate one a smaller number. A later stage shows seven zoœcia (pl. 16, fig. 23), and so on until the colony numbers hundreds of zoœcia. Instances are found in abundance where the shell remains *in situ* until after the branched spines have formed around the margin of the primary

zoœcia, and also many colonies in which zoœcia possessing both types of ornamentation occur, both that characterizing the youthful stages (fig. 25) and that found in the adult stage (fig. 22), so that no doubt can exist that we have here the metamorphosis of the *Cyphonautes* of *M. villosa*.

Microporidae Smitt.

Microporidæ Smitt, 1873.
Membraniporidæ, (part) Busk, 1854.
Microporidæ, Hincks, 1880.

Zoœcia with front wall depressed, calcareous margins elevated.

Micropora Gray.

Flustra, (part), Johnston, 1847.
Micropora Gray, 1848.
Discopora (part) Lamarck, 1856.
Membranipora, (part), Busk, 1854.
Micropora, Smitt, 1873.
Micropora, Hincks, 1880.

Zoarium incrusting. *Zoœcia* with prominent raised margins; front wall depressed, wholly calcareous; *orifice* semi-circular or suborbicular, inclosed by a raised calcareous margin.

47. **Micropora coriacea** Esper.

Pl. 17, fig. 26.

Flustra coriacea Esper, 1791-97, pt. 7, fig. 2.
Membranipora coriacea, Busk, 1854, pt. 2, p. 57, pl. 73, figs. 4, 5.
Micropora coriacea Gray, 1848.
Discopora coriacea, Lamarck, 1856, ed. 2, vol. 2, p. 251.
Micropora coriacea, Smitt, 1873, pt. 2, p. 13, pl. 3, fig. 74.
Micropora coriacea, Hincks, 1880, p. 174, pl. 23, figs. 5-7.

Zoarium forming a delicate incrustation on shells, other bryozoa, etc. *Zoœcia* elliptical or rhomboidal (pl. 17, fig. 26); *margin* slightly roughened, raised, sometimes slightly thickened on each side just below the orifice; front wall minutely granular and punctate, frequently possessing a *foramen*, *for.*, a more depressed, thinner portion of the front wall on each side just below the orifice. *Orifice* broader than high, its upper margin semi-circular, its lower margin straight, projecting slightly outward. Occasionally a small *avicularium* just above the orifice, placed some-

what obliquely, mandible directed upward. *Oœcia* subimmersed, large, minutely punctate, sometimes possessing a slight projection in front.

The avicularia are rarely present, and the thickened extremities of the margins which in some cases are said to be prominent tuberosities, do not acquire a great size in the specimens examined. The oœcia are perhaps more deeply immersed than is shown in the drawing.

Micropora coriacea was obtained on the west side of the island of Santa Catalina, dredged at 45 fathoms.

Steganoporellidae Hincks.

Steganoporellidæ Hincks, 1887.

Zoœcia closed by a membranous wall which carries the orifice and operculum; divided by a horizontal calcareous lamina or *cryptocyst* into two compartments, in the lower of which the polypide is lodged; at the distal or oral end of each zoœcium a large variously shaped opening.

Thalamoporella Hincks.

Thalamoporella, Hincks, 1887, vol. 19, p. 164.

Zoœcia in which the lower compartment contains a flask or vase-shaped chamber formed by the *cryptocyst*, in which the polypide resides and through whose narrow neck it protrudes when expanded; on each side of the neck a lateral cavity or foramen; covered only by the membranous front wall. *Orifice* large, only partially closed by the operculum. *Operculum* small, semi-circular. *Oœcia* external, bilobate.

Thalamoporella, and at least one other genus of this family *viz.*, *Steganoporella*, are characterized by the possession of a well developed *cryptocyst*. The term cryptocyst is applied to the calcareous wall of the zoœcium which forms a layer more or less parallel with the chitinous ectocyst, the outermost layer of the zoœcium. The cryptocyst in the genus *Thalamoporella*, is not complete. In the proximal part of the zoœcium it extends from one lateral margin to the other, but as it approaches the operculum it contracts, its lateral edges bend downward, thus producing a narrow neck (pl. 17, fig. 28, *nk.*), through which the

polypide passes on emergence from the zoœcium. The chamber in which the polypide is contained is thus vase or bottle-shaped, its proximal portion forming the body of the vase, the narrow distal portion the neck. On each side of the neck, between it and the lateral edges of the zoœcium, two foramina, *for.*, are formed. These vary somewhat in size and are covered only by a layer of ectocyst. The anterior rim of the cryptocyst widens so as to unite with the lateral edge of the zoœcium above the foramina, but it fails to unite with the lower or proximal edge of the operculum. In this way a large and variously shaped orifice, *or.*, is formed which is divided into two portions by the lower rim of the operculum, the posterior part, *p. or.*, being covered by the chitinous ectocyst, the anterior part, *ant. or.*, by the operculum, *op.*

The function of the foramina was first recognized by Jullien ('88), who regards them as places of attachment for certain muscles whose contraction depresses the ectocyst, thus exerting a pressure on the fluid within the zoœcium, and bringing about the extension of the polypide. From his study of *Steganoporella*, Harmer ('02) is in complete agreement with this opinion. No detailed study has been made of the species of *Thalamoporella* common in our southern waters, but examination of cleared and stained preparations of the younger and more transparent parts of a colony, plainly shows through the transparent walls of the lateral foramina a large number of muscle fibers, and there is no reason to doubt that the foramina afford a point of insertion for these muscle fibers.

48. **Thalamoporella rozieri** (Audouin) Hincks.

Pl. 17, figs. 27, 27a, 28, 29; pl. 18, fig. 30.

Flustra Rozierii Audouin, Sav. 1811, pl. 8, fig. 9.
Membranipora Rozieri, Busk, 1854, pt. 2, p. 59, pl. 65, fig. 6.
?Membranipora gothica Busk, 1856, p. 176, pl. 7, figs. 5-7.
Steginoporella Rozierii, Smitt, 1873, pt. 2, p. 15, pl. 4, fig. 102.
Steganoporella Rozieri, Hincks, 1880a, vol. 6, p. 379, pl. 16, fig. 3.
Thalamoporella Rozieri, Hincks, 1887, vol. 19, p. 164.
Thalamoporella Rozieri, Waters, 1887, vol. 20, p. 186.

Zoarium of large size, forming foliaceous expansions, incrusting stems and fronds of *fucus* (pl. 17, fig. 27a), or erect, branch-

ing, and articulated (fig. 27). *Zoœcia* oblong, quadrangular, alternate; *margins* broad, separating the rows of zoœcia and frequently rising on each side of the orifice into a blunt process (fig. 28, *bl. pro.*) or "tuberosity," or continued in a curved line around the anterior or oral extremity of the zoœcium. *Orifice* large, occupying about one-third of the front, and consisting of two parts; the anterior portion closed by the *operculum, op.*, the posterior part, *p. or.*, by a continuation of the membranous ectocyst of the zoœcium; the lower two-thirds of the zoœcium covered over most of its surface by a double layer: the membranous ectocyst and the calcareous lamina or *cryptocyst*. *Avicularia* (pl. 18, fig. 30, sp. *av.*) large, each occupying the place of a zoœcium; scattered irregularly over the surface of a colony, although sometimes lying side by side; mandible triangular, bent or hooked at the tip, directed anteriorly. *Oœcia* (pl. 17, fig. 29. *œ*), large, globose, wider than long, often extending half way over the adjacent zoœcia; smooth, carinate, not abundant, but occurring in groups irregularly over the colony; oœcial zoœcia of diminished size.

The habit of growth of this species is characteristic. It is sometimes obtained in its incrusting state only, but usually it combines with this the branching habit of growth. The branches are divided into internodes by joints consisting as in *Cellaria* of undeveloped zoœcia in whose walls no calcareous deposit is laid down. The outlines of the zoœcia, however, are plainly discernible in them. These branching tufts are sometimes large, one being found on the beach at San Pedro, California, consisting of a roll of intertwining branches twenty centimeters long and seven and a half centimeters in its greatest diameter.

Hincks ('80a) distinguishes three so-called "forms" of *T. rozieri*, depending upon the possession or non-possession of avicularia, oœcia, and tuberosities. He remarks that there is doubt that these differences are of specific value, and any one who has had the opportunity to examine a large quantity of material must not only concur with this opinion, but doubt also their "form" value. According to Hincks, the normal type of *T. rozieri* possesses oœcia and tuberosities, but no avicularia; the "form" *indica* possesses avicularia and oœcia, but no tuberosities; the "form" *gothica* possesses avicularia and tuberosities, but no oœcia. In our collection, the specimens from La Jolla correspond to the

"form" *indica;* while those from San Pedro agree with no one of the "forms," either the type or otherwise since in different parts of the same colony avicularia, oœcia, and tuberosities or blunt processes are found. The *oœcia,* however, are typical, as are the blunt processes and there seems to be no good reason to consider these colonies as other than unusually fine specimens of the cosmopolitan species *T. rozieri.* Hincks reports the "form" *gothica* as abundant at Santa Monica, California, whose beach is directly continuous with that of San Pedro and whose fauna is almost identical. The mere absence of oœcia is too slight a character on which to base a difference especially when the oœcia occur only in scattered groups and so might not be found unless one had abundance of material. The original "form" *gothica, viz., Membranipora gothica* Busk, was obtained from Lower California, and Busk ('56) found two knob-like structures "at the bottom of the cell (zoœcium) in front" which he considered represent the ovicell. The correctness of this conjecture is, however, doubtful, and taken in connection with all the evidence it is probable that *M. gothica* is a synonym of *T. rozieri.*

T. rozieri is abundant at San Pedro, California, found on sea weed at low tide and off shore at a depth of a few fathoms; it has been frequently obtained at various points of the San Diego region.

Cribrilinidae Hincks.

Celleporidæ Johnston, 1847.
Escharellidæ, d'Orbigny, 1851.
Membraniporidæ, Busk, 1854.
Cribrilinidæ Hincks, 1880.

Zoarium incrusting or erect. *Zoœcia* having the front wall more or less fissured, or traversed by radiating furrows.

Cribrilina Gray.

Cribrilina Gray, 1848, p. 147.
Lepralia (part) Johnston, 1847.
Reptescharella d'Orbigny, 1851.
Escharipora Smitt, 1867.
Cribrilina, Smitt, 1873.
Cribilina, Hincks, 1880.

Zoarium incrusting. *Zoœcia* contiguous, having the front wall more or less occupied by transverse or radiating, punctured furrows. *Orifice* semi-circular or sub-orbicular.

49. **Cribrilina hippocrepis** Hincks.

Pl. 18, fig. 31.

Cribrilina hippocrepis Hincks, 1882, vol. 10, p. 470, pl. 20, figs. 6, 6a.
Cribrilina annulata, Robertson, 1900, p. 326.

Zoarium incrusting shells, worm tubes, etc. *Zoœcia* irregularly alternate, oblong; front wall calcareous, slightly convex, punctured by lines of pores lying in shallow grooves between the radiating ridges (pl. 18, fig. 31); first row of pores immediately below the orifice extending usually across the zoœcium from side to side; the remaining rows, five in number, as a rule, radiating from a point midway between the lower margins of the operculum and the base of the zoœcium. At the origin of each ridge, near the margin, a rather large pore. *Orifice* well arched above, constricted a little above the lower margin which is straight; closed by a dark chitinous *operculum, op. Avicularia, av.*, large, as long as a zoœcium, but narrower, and occupying the place of one; surrounded by a calcareous margin, mandible acutely pointed and directed upward or outward toward the distal edge of the colony. *Oœcia* globose, of medium size, punctured with a few large pores.

Cribrilina hippocrepis is reported by Hincks from Queen Charlotte Islands. That observer found no oœcia in the specimens examined by him, but these structures were obtained in material dredged at San Pedro. This species occurs at Yakutat, Alaska, and at San Pedro and Coronados Islands, California.

Microporellidae Hincks.

Celleporidæ (part) Johnston, 1847.
Membraniporidæ (part), Busk, 1854.
Poridæ (part) d'Orbigny, 1850-52.
Eschariporidæ Smitt, 1867.
Microporellidæ Hincks, 1880.

Zoœcia adnate, incrusting, or forming erect and foliated or dendroid *zoaria; orifice* more or less semi-circular, with the lower margin entire; a semilunar or semi-circular pore on the front wall.

Microporella Hincks.

Eschara, (part) Pallas, 1766.
Lepralia (part) Johnston, 1847.
Lepralia (part), Busk, 1854.
Reptoporina d'Orbigny, 1850-52.
Porellina Smitt, 1873.
Microporella Hincks, 1877.

Zoarium incrusting. *Zoœcia* with a semi-circular orifice, the lower margin entire, and a semilunar or circular pore below it.

50. **Microporella californica** (Busk) Hincks.

Pl. 18, figs. 32, 33, 34.

Lepralia californica Busk, 1856, p. 310, pl. 11, fig. 6.
Microporella ciliata form *californica,* Hincks, 1883, p. 444, pl. 17, fig. 3.

Zoaria forming spinous patches on seaweed (pl. 18, fig. 32). *Zoœcia* ovate or rhomboidal, separated by well marked sutures, alternate (fig. 33); front wall convex, calcareous, punctate. *Orifice* arched above, lower margin straight; upper margin surrounded by six or seven long spines, in some cases small and dark in color; below the orifice an oval or sometimes obscurely lunate pore filled in with a fine sieve-like plate (fig. 34); the pore frequently hidden more or less by an umbonate process (fig. 33, *um. pro.*) developed just below it; or the pore may be somewhat elevated. On each side of the pore a sessile *avicularium* with mandible directed obliquely upward or slightly outward. *Oœcia* globose, of medium size, punctate, where spines are present on the zoœcium, the lowermost pair visible in front of each oœcium.

Hincks regards this as a form of the cosmopolitan species *M. ciliata* and reports it as abundant at Queen Charlotte Islands. The chief differences between *M. californica* and the typical *M. ciliata* lie in the possession by the former of an avicularium on each side of the median pore instead of upon one side only, and in the structure of the plate covering the pore. In *M. ciliata* the pore is semilunate, the inner edges of the crescent being furnished with fine teeth, the whole strongly resembling the pore of *M. malusi* (fig. 35, *p.*). In *M. californica* the pore is large, oval, and

surrounded by a definite border, the upper or distal portion of which sometimes dips inward slightly, making it very obscurely lunate. The space within the border is completely filled with an oval plate in which are several minute pores, the plate being in reality a sieve (fig. 34). The shape and structure of this median pore are thus very different from that of *M. ciliata,* and its peculiar features are constant in the specimens examined and are considered sufficient to constitute a species as Busk first described. Typical *M. ciliata* does not occur in this collection.

M. californica is quite abundant, having been found at numerous points on the coast of southern California especially, generally in conjunction with *Schizoporella hyalina.*

51. **Microporella malusi** (Audouin) Hincks.

Pl. 18, figs. 35, 36.

Cellepora Malusii Audouin and Savigny, 1811, p. 239, pl. 8, fig. 8.
Lepralia Malusii, Johnston, 1847, ed. 2, p. 314, pl. 55, fig. 4.
Reptoporina Malusii, d'Orbigny, 1850-52, p. 443.
Lepralia Malusii, Busk, 1854, pt. 2, p. 83, pl. 103, fig. 1-4.
Lepralia Malusii, Busk, 1859, p. 53, pl. 8, fig. 3.
Lepralia Malusii, Waters, 1879, vol. 3, p. 33.
Mieroporella Malusii, Hincks, 1880, p. 211, pl. 28, figs. 9-11; pl. 29, figs. 1, 2.
Microporella Malusii, Busk, 1884, pl. 30, vol. 10, p. 137.
Fenestrulina Malusii, Jullien, 1888, p. 38, pl. 15, figs. 1-3.

Zoaria forming circular patches incrusting old stems, rocks, etc. *Zoœcia* irregularly ovate or rhomboidal, alternate, radiating from a central point; front wall calcareous, punctate, slightly convex, margins well defined (fig. 35); immediately inside the margin a row of stellate pores; the center of the front wall occupied by a large semi-circular pore whose edges are irregularly toothed. *Orifice* straight below, semi-circular above, with four or five marginal spines; *spines* prominent on the marginal zoœcia and present, though frequently broken, on the margin of intermediate zoœcia. *Oœcia* globose, partially covering the lunate pore of the zoœcium next above, and surrounded by an areolated border. The primary zoœcium (fig. 36), that from which the colony originates, is circular in form, its margin surrounded by ten flaring spines.

This species is reported by Hincks from Queen Charlotte Islands, where it is said to be abundant. In our collection it has been obtained at La Jolla growing on roots of kelp, and dredged between 20 and 30 fathoms off Catalina Islands.

Porinidae (part) d'Orbigny.

Membraniporidæ, (part) Busk, 1854.
Eschariporidæ Smitt, 1867.
Porinidæ Hincks, 1880.

Zoarium incrusting, or erect and ramified. *Zoœcia* with a raised tubular or subtubular *orifice*, and frequently with a special pore on the front wall.

Lagenipora Hincks.

Lagenipora Hincks, 1877.
Lagenipora Hincks, 1880.
Lagenipora Hincks, 1884.

Zoaria consisting of a number of zoœcia immersed in a common-calcareous crust, or rising into branching masses. *Zoœcia* in the incrusting state, decumbent, lageniform; oral extremity free, tubular, with a terminal *orifice*.

The free, tubular portion of the zoœcium in *Lagenipora* is known as a peristome, a structure frequently found in the more highly calcified *Chilostomata*. The *peristome* is a secondary calcareous wall of varying height, and surrounding the original or primary orifice of the zoœcium more or less completely. It thus forms a secondary orifice which as in *L. spinulosa* (pl. 18, fig. 37) may be ornamented by numerous spines and may rise so high above the primary orifice as to hide it completely; or it may be a narrow or slightly thickened rim of the primary orifice so low as to be scarcely recognized as a secondary orifice. The peristome, especially when well developed, affords a diagnostic mark of some importance.

52. **Lagenipora spinulosa** Hincks.

Pl. 18, fig. 37.

Lagenipora spinulosa Hincks, 1884, vol. 13, p. 57, pl. 3, fig. 4.
Lagenipora spinulosa Hincks, 1884, vol. 13, p. 210, pl. 9, fig. 4.

Zoarium incrusting, or erect and branching. *Zoœcia* lageniform, lower portion adherent, ovate, thickly covered with large

pores; upper or oral portion free, tubular, produced, expanded toward the oral rim, suberect, surface smooth, hyaline (pl. 18, fig. 37). *Orifice* terminal, sometimes a shallow sinus, *s.*, formed partly by the high avicularian peduncles rising on each side, partly by the flaring outward and forward of the frontal wall of the tubular portion or peristome; dorsal wall of tubular portion flaring outward and bordered by five to seven long, delicate *spines.* A small sessile *avicularium, av.*, on each side of the orifice, elevated on a peduncle which is sometimes of extraordinary height, mandible pointed and directed away from the orifice; usually a denticular process, *d.*, on the peduncle below the avicularium. *Oœcium, oc.*, small, rounded, smooth except for a wide band extending across the front which is thickly punctate; set far down at the back of the tubular portion of the zoœcium; the avicularian peduncles and sometimes a portion of the front tubular wall often rising in front of the oœcium almost completely hiding it when viewed from the front.

This beautiful species is described by Hincks from Queen Charlotte Islands. Both description and plate suggest that that observer possessed only mutilated colonies. In the unmutilated state the spines are extremely delicate and in protected positions they attain an extraordinary length; the tubular portion of the zoœcium also is easily and frequently broken. The avicularian peduncles are often much longer than they are represented in the drawing (fig. 37 *av.*).

Lagenopora spinulosa has been rarely obtained, a few small colonies having been found on *Retepora pacifica* from Catalina Island, and a specimen of the erect form from Pacific Grove, California.

Myriozoidae (part) Smitt.

Celleporidæ (part) Johnston, 1847.
Porinidæ (part) d'Orbigny, 1850-52.
Membraniporidæ (part), Busk, 1854.
Myriozoidæ (part) Smitt, 1867.

Zoarium incrusting, or rising into foliaceous expansions, or dendroid. *Zoœcia* calcareous, destitute of a membranous area and raised margins. *Orifice* with a sinus on the lower lip.

Schizoporella Hincks.

Lepralia (part) Johnston, 1847.
Reptoscharella d'Orbigny, 1850-52.
Schizoporella Hincks, 1880.

Zoarium incrusting, or forming foliaceous expansions. *Zoœcia* with a semi-circular or suborbicular orifice, the lower margin with a central sinus. *Avicularia* usually lateral, sometimes median, with an acute, or rounded, or spatulate mandible; occasionally wanting.

KEY TO SPECIES OF SCHIZOPORELLA.

1. Zoœcia with avicularia 9
1. Zoœcia without avicularia 2
2. Zoœcia elongated 3
2. Zoœcia not elongated 6
3. Sinus shallow 4
3. Sinus distinct, sometimes shallow 5
4. Zoœcia with front wall porous ..... **S. insculpta**
4. Zoœcia with front wall not porous 5
5. Front wall marked by transverse ridges or lines ..... **S. hyalina**
6. Zoœcia rhomboidal 7
6. Zoœcia not rhomboidal 8
7. Sinus shallow ..... **S. areolata**
7. Sinus distinct 8
8. Oœcia smooth ..... **S. cecili**
8. Oœcia porous ..... **S. linearis** var. **inarmata**
9. Avicularia on one side of the orifice only 10
9. Avicularia on both sides of the orifice ..... **S. biaperta**
9. Avicularia median 12
10. Zoœcia with whole surface porous 11
10. Zoœcia with marginal pores only 12
11. Avicularia with mandible directed downward ..... **S. longirostrata**
11. Avicularia with mandible directed upward 12
12. Zoœcia with an umbo below the orifice ..... **S. oligopus**
12. Zoœcia without an umbo, but frequently with an avicularium below the orifice ..... **S. tumulosa**
13. Avicularia with mandible rounded or oval ..... **S. auriculata**

53. **Schizoporella areolata** Busk.

Pl. 18, fig. 38.

Lepralia areolata Busk, 1854, pt. 2, p. 82, pl. 83, figs. 3, 4.

Zoarium forming a rather thick calcareous crust over sponge. *Zoœcia* large, subovate or diamond shaped, alternate, outline of each distinctly marked; front wall slightly convex and thickly

covered with large pores. *Orifice* large, semi-circular above, lower margin with a shallow sinus somewhat extended in front; surrounded by a thickened peristome. *Avicularia* none. *Oœcium* unknown.

The orifice of this species is considerably larger than that of the typical Schizoporella, but the possession of a decided sinus on the lower margin places it with this genus. This species was originally described by Busk from the Straits of Magellan obtained at a depth of 10 to 20 fathoms. The specimen from which this identification is made consists of a small piece of a colony which was dredged on the west coast of the island of Santa Catalina, depth not known, probably scraped off of a rocky wall as the dredge came up.

54. **Schizoporella auriculata** (Hassall) Hincks.

Pl. 19, fig. 39.

Lepralia auriculata Hassall, 1842, vol. 9, p. 412.
Lepralia auriculata, Johnston, 1847, ed. 2, p. 310, pl. 54, fig. 8.
Lepralia auriculata, Busk, 1854, pt. 2, p. 67, pl. 89, figs. 4-6.
Schizoporella auriculata, Hincks, 1880, p. 260, pl. 29, figs. 3-9.

Zoarium incrusting. *Zoœcia* rhomboid, sometimes sub-ovate, short, disposed in linear series, radiating from a central point; separated by distinct lines; front wall punctured. *Orifice* small, suborbicular, rounded above, with a definite rather narrow sinus on the lower margin. Spines? A small avicularium (pl. 19, fig. 39) with rounded mandible immediately below the sinus on a slight mamillary eminence. *Oœcia* subglobose, immersed, punctured.

This species was obtained in small quantity off the Coronado Islands dredged in 99.5 fathoms.

55. **Schizoporella auriculata** subsp. **ochracea** Hincks.

Pl. 19, fig. 40.

Lepralia ochracea Hincks, 1861, vol. 9, p. 206, pl. 12, fig. 3.
Schizoporella auriculata, var. ochracea Hincks, 1880, p. 260, pl. 29, fig. 7.

Zoarium incrusting. *Zoœcia* rhomboid, disposed in linear series, radiating from a central point; separated by distinct lines;

front wall punctured. *Orifice* small, rounded above with a definite sinus on the lower margin. Some distance below the sinus, an oval or slightly elongated *avicularium* (pl. 19, fig. 40, *av.*), immersed, or if raised, only very slightly, mandible directed straight downward. *Oœcia* subglobose, small, immersed, punctured.

This sub-species was obtained in small quantity near San Pedro, dredged in 32.5 fathoms.

56. **Schizoporella biaperta** (Michelin) Hincks.

Pl. 19, fig. 41.

Eschara biaperta Michelin, 1841-42, p. 330, pl. 79, fig. 3.
Reptoporina biaperta, d'Orbigny, 1850-52, p. 442.
Lepralia biaperta, Busk, 1859, p. 47, pl. 7, fig. 5.
Escharella linearis, forma *biaperta* Smitt, 1867, pp. 14 and 98, pl. 24, figs. 70, 73.
Hippothoa biaperta, Smitt, 1873, pt. 2, p. 46, pl. 8, figs. 173-176.
Hippothoa divergens Smitt, 1873, pt. 2, p. 47, pl. 9, figs. 177-179.
Lepralia linearis var. *biaperta,* Waters, 1879, vol. 3, p. 37, pl. 11, figs. 1, 2.
Schizoporella biaperta, Hincks, 1880, p. 255, pl. 40, figs. 7-9.
Schizoporella biaperta, Robertson, 1900, p. 326.

Zoarium forming an irregular crust over the substratum of shells, stems, etc. *Zoœcia* ovate, slightly convex, surface hyaline, punctured in the younger stages, becoming thicker and granular in the older stage, always marked by faint anastomosing lines (pl. 19, fig. 41). *Orifice* circular, with a distinct sinus whose lateral walls are slightly raised; peristome low. On each side of the orifice an elevated *avicularium* with small triangular mandible directed upward; occasionally on the lower part of the zoœcia a larger avicularium, *av.*, elevated upon a rounded prominence. *Oœcia, oc.,* rounded, the front wall flattened and traversed by radiating lines.

The zoœcia bearing the ovicells are not invariably of a different size and appearance from those that do not possess these structures as Hincks ('80) seems to imply. The smaller zoœcia and the mamillated avicularia occur generally in the more

crowded portions of the colony where, for mechanical reasons probably, the zoœcia are unable to assume their typical size and appearance.

This species probably has a wide distribution on this coast. It is reported by Hincks from Queen Charlotte Islands, and in our collection has been obtained from the shore of Alaska, and dredged at 132 fathoms off Point Loma, San Diego. It has not been obtained between these localities.

57. **Schizoporella cecili** (Audouin) Hincks.

Pl. 19, fig. 42.

Flustra Cecilii Audouin (Sav.), 1811, p. 66, pl. 8, fig. 3.
Lepralia Cecilii, Busk, 1857, p. 173, pl. 15, figs. 6, 7.
Lepralia Perugiana Heller, 1867, p. 102, pl. 2, fig. 10.
Lepralia Cecilii, Waters, 1879, vol. 3, p. 30, pl. 8, fig. 6.
Schizoporella Cecilii, Hincks, 1880, p. 269, pl. 43, fig. 6.
Schizoporella Cecilii, Ortmann, 1890, p. 51, pl. 4, fig. 4.

Zoarium forming a delicate crust. *Zoœcia* ovate, distinct, separated by distinct lines, alternate, thickly punctured over the surface, a row of small punctures outlining the margin; *orifice* arched above, lower margin straight with a characteristic loop-like sinus in the middle (pl. 19, fig. 42); peristome slightly raised. *Avicularia* none. *Oœcia* prominent, taller than broad, smooth, convex, granular.

The species here identified as *S. cecili* lacks the smooth umbonate process described by most observers. Waters ('79) describes a species from the Bay of Naples which possesses an imperforate area below the aperture, and points out that this species occurs in the Red Sea and from Kino Channel, Japan, in which neither imperforate area nor umbo are found. He remarks that we may consider that there is a variety with an umbo and one without.

S. cecili is not found in great abundance. A single specimen is reported by Hincks from Queen Charlotte Islands. Only a single small piece of a colony growing over sponge occurs in our collection from San Pedro, California.

58. **Schizoporella hyalina** (Linnæus) Hincks.

Pl. 19, figs. 43, 44, 45.

Cellepora hyalina Linnæus, 1766-1768, ed. 12, p. 1286.
Escharina personata Lamarck, 1856, ed. 2, vol. 2, p. 236.
Lepralia hyalina, Johnston, 1847, ed. 2, p. 301, pl. 54, fig. 1.
Reptoscharella personata, d'Orbigny, 1850-52, p. 465.
Lepralia hyalina, Busk, 1854, pt. 2, p. 84, pl. 82, figs. 1, 2, 3; pl. 95, figs. 3, 4, 5; pl. 101, figs. 1, 2.
Lepralia discreta, Busk, 1854, pt. 2, p. 85, pl. 1, figs. 3, 4.
Lepralia discreta, Busk, 1859, p. 52, pl. 5, fig. 1.
Lepralia hyalina var. *conferta* Busk, 1876, p. 117.
Schizoporella hyalina, Hincks, 1880, p. 271, pl. 18, figs. 8-10; pl. 45, fig. 2.
Diazeuzia hyalina, Jullien, 1888, p. i. 29, pl. 4, figs. 1-4.
Diazeuzia reticulans Jullien, 1888, p. i. 33, pl. 4, fig. 5.
Schizoporella hyalina, Robertson, 1900, p. 326.

Zoaria forming delicate, one-layered, reticulated, circular incrustations on stems and fronds of seaweed; or the zoœcia piling on top of each other in an irregular way, having much the appearance of *Cellepora*. *Zoœcia* variously shaped; in the one-layered condition (pl. 19, fig. 43), subcylindrical, elongated, distinct, disposed in radiating rows and separated by large punctures, giving the whole colony a reticulated appearance; wall thin, delicate, transparent, hyaline; again, the zoœcia may be shorter and more barrel-shaped (fig. 45); with wall more opaque, thicker, white; crossed by transverse lines or ridges (fig. 44), with sometimes a distinct, broad umbo (fig. 45, *um.*) just below the orifice and partially hiding it; *orifice* often orbicular, wide, without a sinus except as the denticles (fig. 45, *d.*) projecting on each side define a rather shallow sinus; again the orifice may be large (fig. 44, *or.*) with or without a well marked sinus *s.*; peristome, if present, thin, only slightly elevated on the upper margin. *Oœcia* large, globose; in the more delicate, hyaline condition (fig. 43) either imperforate, or with pores around the margin; in the form with transverse ridges (fig. 44), marked by corresponding circular ridges, pores few, scattered, sometimes an umbo, *um.*, in the middle of the oœcial wall; in the more opaque variety, oœcia (fig. 45) with scattered pores; oœcial zoœcia usually smaller than the ordinary ones.

This protean species assumes many forms in our waters such that if the extremes only, or isolated specimens are examined they appear to be different species. Transition stages, however, occur between the numerous variations, and it has not been thought best to divide the species. Taking the whole coast from Alaska to San Diego, the delicate, hyaline, strongly reticulated (fig. 43) colonies are more common in the south; these may or may not have the lateral processes described as var. *cornuta* by Busk ('54) and Hincks ('80). Even in the south, *i.e.*, south of Point Conception, the thicker walled variety occurs in small quantity. This is frequently strongly reticulated, often has the lateral processes, and is usually marked by definite transverse lines with an umbo below the orifice; it sometimes forms colonies of more than one layer, the upper layers of zoœcia becoming very irregular in arrangement. North of San Francisco Bay, the thicker walled variety is very abundant. Here the zoœcia of the first layer are often much elongated, well separated and with or without reticulations; sometimes they are more barrel-shaped, having well marked transverse lines and ridges and frequently a distinct umbo below the orifice. Since in a study of specimens from the whole coast the marks characteristic of the var. *cornuta* and of the species *S. discreta* are found mingling together and merging almost insensibly, there is no sufficient ground upon which to base sub-species and all are reported here under the one name.

The typical *S. hyalina* together with var. *cornuta* are reported by both Busk and Hincks from California. Reported also from Queen Charlotte Islands. Abundant in our collection from Yakutat, Alaska, to San Diego, California, found between tide marks.

59. **Schizoporella insculpta** Hincks.

Pl. 20, figs. 46, 47.

Schizoporella insculpta Hincks, 1882, vol. 10, p. 252.
Schizoporella insculpta Hincks, 1883, vol. 11, p. 447, pl. 17, fig. 5, 5a.
Schizoporella insculpta, Robertson, 1900, p. 326.

Zoarium incrusting, or rising into foliaceous, bilaminate expansions. *Zoœcia* large, elongated, alternate, separated by distinct lines; front wall thickly covered with large pores. *Orifice*

rounded above, the lower margin almost entirely occupied by a wide shallow sinus (pl. 20, fig. 46); *peristome* thin, moderately raised, sometimes extended in front beyond the sinus. *Oœcia* (fig. 47) abundant, large, covering two-thirds and often more of the zoœcium above; oral arch high, oœcial wall covered with granular ridges radiating from the oral arch: generally punctured around the base. *Avicularia* none.

This species described by Hincks from Queen Charlotte Islands, is common in Puget Sound and on the coast of California as far south as Coronados Islands, at which place it has been dredged at a depth of 18 fathoms. Abundant on the shore at Pacific Grove, California. Found also as far north as Sitka, Alaska.

60. **Schizoporella linearis** Hassall, subsp. **inarmata** Hincks.

Pl. 20, fig. 48.

Schizoporella linearis form *inarmata* Hincks, 1884, vol. 13, p. 212.
Lepralia linearis, Waters, 1879, vol. 3, p. 38, pl. 9, fig. 2.

Zoarium incrusting shell of barnacle. *Zoœcia* rhomboidal, disposed in linear series, separated by distinct lines, or sometimes confluent, and forming a uniform crust (pl. 20, fig. 48); front wall flat, nodulous, or covered with anastomosing ridges, and punctate, or enveloped in a granular crust; *orifice* orbicular, peristome raised, a sinus on the lower margin. *Oœcia* globose, prominent, thickly punctured, anastomosing lines proceeding from a median line extending from the oral to the distal rim.

The sub-species *inarmata* differs from the ordinary form mainly in the lack of avicularia which in the typical *S. linearis* are found on each side of the orifice.

Reported by Hincks from Queen Charlotte Islands. Obtained at one station on the west side of the island of Santa Catalina dredged in 45 fathoms.

61. **Schizoporella longirostrata** Hincks.

Pl. 20, fig. 49.

Schizoporella longirostrata Hincks, 1883, vol. 11, p. 447, pl. 15, fig. 4.

Zoarium forming a delicate white crust over shells of barnacles, etc. *Zoœcia* large, ovate, moderately convex, surface gran-

ular with pores scattered irregularly over it (pl. 20, fig. 49); often a row of pores on each side near the margin. *Orifice* arched above, with a wide shallow sinus on the lower margin; lateral denticles well developed; *peristome* thin, slightly elevated. On one side of each zoœcium, a little below the orifice, an elevated *avicularium* with much elongated and acutely pointed mandible directed downward. *Oœcium* small, slightly higher than wide, surface granular, punctate, oral arch shallow.

This species is described and reported by Hincks from Queen Charlotte Islands. It is fairly abundant in the California fauna, being obtained at several points near San Pedro and Catalina Islands.

62. **Schizoporella oligopus** sp. nov.

Pl. 20, figs. 50, 51, 52.

Zoarium having a delicate, hyaline appearance and forming a single layered incrustation attached to the substratum by means of numerous calcareous prolongations resembling tube feet (pl. 20, fig. 50, *tu. ft.*), extending from the under side. *Zoœcia* ovate, or of irregular shape, having a definite thickened margin inside of which is a row of large pores (fig. 51); front wall convex, rising into a distinct umbo, *um.*, below the orifice, and thickly covered with papillæ instead of the usual punctures. *Orifice* rounded above, with a shallow sinus on the lower margin. To one side of the orifice, an *avicularium* on a high mound, the lower edge of which has a row of large pores similar to those inside the zoœcial margin; its surface covered with minute papillæ similar to those on the zoœcial wall; mandible directed outward, the outer edge of the mound rising in a point and curving over the tip of the mandible; avicularium not present on every zoœcium. *Oœcium* (fig. 52, *oe.*) large, a thin calcareous rim on the oral margin; the margin by which it unites with the zoœcium above crenate; crenations thickly covered with papillæ; convex surface of oœcium thickly punctured, but showing minute papillæ between the punctures. The under surface (fig. 50) of each zoœcium slightly convex, smooth, giving off a number of tubular prolongations arising either on the margin of a zoœcium or from any portion of the

surface; number varying between three and five depending on the size and shape of the zoœcia.

The possession of adherent calcareous tubes allies this species to *Schizoporella argentea* Hincks ('85). Of this species Hincks writes, "set round the edge are six prominent tubular projections with which probably some chitinous appendage may be connected. On the sutures between the cells (zoœcia) are six rather large foramina which pierce through the zoarium and open out on the front surface, so that the zoœcia may be regarded as to some extent, disjunct, and attached to one another by six broad connecting processes (pl. 9, fig. 6*a*)." In *S. oligopus* there is no indication of a chitinous appendage to the tube feet. However, the portions of the colony from which this description is written were not obtained *in situ*, so that the sort of substratum upon which it grew as well as the sort of adherence is unknown. Each tubular prolongation is lined by a continuation of the epithelium lining the zoœcium, and in some cases this epithelium is pulled out into a long process (fig. 50, *ep. pro.*) beyond the tube foot, supposedly by the force separating it from the substratum. At the angles formed by the union of three zoœcia, foramina (fig. 51, *for.*) are sometimes found piercing the zoarium, but these are not as numerous nor as constant as are those of *S. argentea*.

It is a question whether or not the peculiar method of adherence characteristic of these two species *S. oligopus* and *S. argentea* may be sufficient to remove them from the present genus. However, it is not considered advisable to do so, until more material is obtained and until the zoarium is found *in situ* and its growth habit carefully studied.

Schizoporella oligopus was dredged in the vicinity of San Pedro, California.

63. **Schizoporella tumulosa** Hincks.

Pl. 20, fig. 53.

Schizoporella tumulosa Hincks, 1883, vol. 11, p. 447, pl. 18, fig. 2.

Zoarium forming a thick, white, calcareous crust over shells. Often growing several layers thick, one on top of the other, the calcareous deposit becoming thicker with each layer. *Zoœcia*

large, ovate, front wall much elevated in the middle and sloping down to the lateral margins and toward the base; wall dense, smooth, areolated round the edge, in younger colonies the areolæ large with tube-like ridges radiating toward the middle (pl. 20, fig. 53). *Orifice* circular, with a shallow sinus on the lower margin; *peristome* low; with increase of calcareous deposit, the orifice comes to be sunken deeply. Below the orifice and to one side an *avicularium*, *av.*, much elevated, forming a mound, *av. m.*, or rounded prominence which partially hides the orifice; mandible, *man.*, bent at the tip, narrow, directed outward, or upward; a short, mucronate process, *mu. pro.*, where the tip of the mandible closes into the beak. In older parts of the colony, zoœcia shorter, calcification increased and an avicularium with mandible directed downward in the middle of the front wall. *Oœcia* smooth, broader than high, almost covered by the elevated avicularium on the lower part of the zoœcium above.

The oœcia occur only on the older portions of the colony and each is not only immersed behind the mound of the avicularium above it, but is surrounded by these structures, there being one above the oœcium, one below, and one on each side. Avicularia are scattered profusely over the whole surface of old colonies.

This species described by Hincks from Queen Charlotte Islands. Fairly abundant in dredgings from San Pedro to San Diego.

Myriozoum Donati.

Myriozoum Donati, 1751.
Millepora (part) Pallas, 1766.
Myriapora Blainville, 1834.
Myriozoum, Busk, 1873-76.
Myriozoum, Hincks, 1877.

Zoarium incrusting, or erect, branched; branches cylindrical, obtuse; surface punctured or reticulate. *Avicularia* when present, immersed. *Orifice* with a sinus on the lower margin.

The three *Myriozoa* of the Pacific coast assume two habits of growth very unlike each other. One species, *M. crustaceum*, is an incrusting form, never as far as I know, becoming upright. The other two species, *M. coarctatum* and *M. subgracile* begin as in-

crusting colonies, but soon grow into stiff, upright, branching stems (pl. 21, fig. 57). The older portions of these colonies become highly calcified, and the active zoœcia are found only at the rounded tips of the branches. The arrangement of the zoœcia in such stem is regularly alternate around a central core (fig. 56). The inner zoœcial walls have an extremely delicate finely porous structure, while the external walls are generally more coarsely porous or reticulated.

64. **Myriozoum crustaceum** Smitt.

Pl. 21, fig. 54.

Myriozoum crustaceum Smitt, 1867, p. 18, pl. 25, figs. 88-91.
Myriozoum crustaceum, Robertson, 1900, p. 327.

Zoarium incrusting, often growing in several layers one on top of the other. *Zoœcia* immersed, lines of separation not visible, front wall thickly punctate, or in a younger stage, reticulate (pl. 21, fig. 54). *Orifice* rounded above, the lower margin possessing a well marked sinus. Usually a small avicularium, *av.*, on each side of the orifice, sometimes on one side only. *Oœcium* of moderate size, sub-immersed, bordered with a row of pores and thickly punctate.

This species has been obtained at Yakutat, Orca, Kadiak and Juneau on the coast of Alaska.

65. **Myriozoum coarctatum** Sars.

Pl. 21, figs. 55, 56, 57.

Myriozoum coarctatum Sars, 1851, vol. 6, p. 148.
Myriozoum coarctatum, Smitt, 1867, p. 18, pl. 25, fig. 92.

Zoarium ramose, attaining a height of 75 to 100 mm.; branching dichotomous. *Zoœcia* immersed, alternate, front wall thickly covered with large pores (pl. 21, fig. 55). *Orifice, or.*, higher than broad, rounded above, lower margin possessing a well formed sinus. *Avicularia* wanting. *Oœcia?*

This species is reported by Hincks from Queen Charlotte Islands. Dredged at 20 fathoms at Juneau; found also at Orca and Yakutat, Alaska.

66. **Myriozoum subgracile** d'Orbigny.

Pl. 21, fig. 58.

Myriozoum subgracile d'Orbigny, 1850-52, p. 662.
Myriozoum subgracile, Smitt, 1867, p. 48.
Myriozoum subgracile, Hincks, 1877, p. 106.

Zoarium ramose, having much the same general appearance as the foregoing species, branches slimmer, less robust. *Zoœcia* immersed, alternate, front wall granular not punctate (pl. 21, fig. 58), except at the base of the colony where the zoœcia are hidden under a calcified porous layer. *Orifice*, *or.*, higher than broad, rounded above, lower margin straight and possessing a well marked sinus. A small *avicularium*, *av.*, above each zoœcium, mandible directed obliquely downward. *Oœcia?*

This species has been obtained in but one locality, appearing in the collection from San Juan Co., Puget Sound. These specimens possess but one avicularium above the zoœcium, although a specimen examined from Baffins Bay has two small avicularia above each zoœcium.

Hippothoa Lamouroux.

Mollia (part) Smitt, 1867.
Hippothoa, Busk, 1852.
Hippothoa, Hincks, 1880.

Zoarium forming a delicate tracery on stones, roots, etc. *Zoœcia* minute, distant, caudate, connected with one another by a slender prolongation of the posterior part of the zoœcium so as to form a linear series; branches given off from the sides of the zoœcia; *orifice* subterminal, suborbicular, with the lower margin sinuated or produced.

67. **Hippothoa divaricata** Lamouroux.

Pl. 21, figs. 59, 60.

Hippothoa divaricata Lamouroux, 1821, p. 82, pl. 80, figs. 15, 16.
Hippothoa divaricata, Johnston, 1847, p. 291, pl. 51, figs. 3, 4.
Hippothoa divaricata, Busk, 1852, p. 30, pl. 18, figs. 3, 4.
Hippothoa patagonica Busk, 1852, p. 30, pl. 17, fig. 1.
Mollia divaricata, Smitt, 1867, p. 17 and 112, pl. 25, figs. 86, 87.
Hippothoa divaricata, Hincks, 1880, p. 288, pl. 44, figs. 1-4; pl. 1, fig. 2.

Zoarium forming a delicate, branching tracery; branches arising from the summit or side of zoœcia (pl. 21, fig. 59). *Zoœcia* tubular below, expanding above, elongated, ovate, more or less distant, sometimes growing in close patches lying together irregularly, sometimes quite remote from each other; finely striated, subcarinate in front (fig. 60); *orifice* arched and raised above with a sinus on the lower margin. *Oœcia, oc.*, small, globose, with a boss or umbo, *um.*, in front, borne on a lateral zoœcium inferior in size to the ordinary ones.

This species is probably abundant, but it is so inconspicuous as to escape observation easily. It occurs at various localities on our southern coast between tide marks.

Escharidae (part) Smitt.

Celleporidæ (part) Johnston, 1847.
Escharidæ (part) Smitt, 1867.
Membraniporidæ (part) Busk, 1854.
Escharidæ, Hincks, 1880.

Zoarium calcareous, incrusting, erect, and lamellate, or ramose. *Zoœcia* without a membranous area or raised margins: (a) with a simple primary aperture, horseshoe-shaped, semielliptical, or suborbicular; or (b) with an elevated secondary orifice inclosing an avicularium; or (c) with a primary orifice having a dentate lower margin and a secondary orifice channelled in front or entire; or (d) with the lower margin elevated into a mucro; in all cases destitute of a true sinus and special pores.

As Hincks remarks, this is a somewhat miscellaneous group of forms. They are, as a rule, characterized by the possession of one or more denticles, or an avicularium inside the peristome. This is not true of *Lepralia*, however, which seems to be included here because it does not fit anywhere else. The genus *Lepralia* is not common in this fauna, there being but one species so far known.

KEY TO THE GENERA OF ESCHARIDÆ.

1. Those with simple orifice..... **Lepralia**
1. Those with a secondary orifice..... 2
2. Those in which the secondary orifice is channelled in front..... 3
2. Those in which secondary orifice is not channelled in front..... 5

3. Those in which the peristome incloses a tooth or an avicularium.... 4
3. Those in which there is no inclosure.....**Retepora**
4. Those in which the peristome incloses an avicularium..... 7
4. Those in which the peristome incloses a tooth.....**Smittia**
5. Those with secondary orifice rising into a mucro.....**Mucronella**
5. Those in which the secondary orifice does not rise into a mucro..... 6
6. Those in which peristome is entire.....**Phylactella**
7. Avicularium with rounded mandible.....**Porella**
7. Mandible of avicularium not rounded.....**Escharoides**

Lepralia (part) Johnston.

Lepralia Johnston, 1847.
Lepralia (part), Busk, 1854.
Lepralia, Hincks, 1880.

Zoœcia usually ovate, with the *orifice* more or less horseshoe-shaped, arched above, contracted at the sides, with the lower margin entire and generally slightly curved outward. *Zoarium* incrusting, or rising into foliated expansions composed of one or two layers.

68. **Lepralia bilabiata** Hincks.

Pl. 21, figs. 61, 62, 63, 64.

Lepralia bilabiata Hincks, 1884, vol. 13, p. 49, pl. 3, figs. 1, Ia, Ib.

Zoarium forming a thick one-layered crust over stems or shells, red in life, turning brown when placed in alcohol. *Zoœcia* short and broad, alternate, rounded above, truncate below; the front wall at the outer growing rim almost wholly membranous (pl. 21, fig. 61, *im. zoe.*) soon covered over somewhat more than half its surface by a delicate calcareous front wall, granular, white, convex; in older zoœcia (fig. 62), rising into a keel, *k.*, extending from the lower rim of the operculum to the base of the zoœcium, and forming a thick rim, *th. r.*, above the large operculum, *op.* Zoœcia separated by faint, scarcely perceptible brown lines, front wall marked by radiating striæ and sometimes rising into a distinct umbo, *um.* *Operculum* large, brown, occupying almost half the front surface of the zoœcium, semicircular above, with a strong rib on the edge; curved on the lower margin, where it is also strengthened by a chitinous bar; the true orifice (fig. 63, *or.*) inside the outer brown operculum, *ou. op.*,

and guarded by two chitinous lips. *Oœcia* immersed (fig. 64, *oe.*), formed by an extension of the zoœcial wall above the operculum and marked by a large pore, *p.*, covered with a chitinous membrane. *Avicularia* none.

The orifice in *Lepralia bilabiata* is characteristic and deserves closer inspection. Unlike that of the usual *Chilostomatous* zoœcium the orifice here is not closed directly by the external operculum. When dissected out (fig. 63), the orifice is seen to be closed by two chitinous ribs, the one, *rb'.*, forming the distal edge of a thin, chitinous membrane lying against the inner side of the oral extremity of the zoœcium and forming what may be regarded as a dorsal or inner operculum, *in. op.* This is ordinarily hidden by the external operculum when the polypide is retracted and the orifice closed. The other, the ventral or outer operculum, *ou. op.*, consists of a relatively thick, chitinous membrane surrounded by a strong chitinous framework. At its distal extremity there is a folded membrane, *fd. mem.*, possessing on its inner side a chitinous rib, *rb.*, forming the outer or ventral lip of the orifice or mouth, *or.* The inner rib, *rb'.*, and the outer rib, *rb.*, are continuous at the corners forming a narrow elongated mouth through which the polypide emerges. Extending from the corners of the mouth between the lateral edges of the inner and outer opercula is a lateral membrane, *lat. mem.*, connecting them, the whole forming the tube mentioned by Hincks ('84), through which the polypide passes as it emerges from the zoœcium. When closed, the outer operculum shuts down upon the two lips of the orifice, making a sort of third or accessory lip, *ac.*

If we regard the outer operculum as homologous with the ordinary *Chilostomatous* operculum, then its function has changed considerably. Instead of primarily effecting the closure of the orifice, it does so only secondarily by its connection with the folded membrane forming the ventral lip. In this case the inner operculum and the oral lips are new structures peculiar to this species.

Hincks remarks that the entrance to the oœcium is closed by the operculum. The ovicells are not abundant in this material and this point could not be satisfactorily verified. There is a possibility that the pore may be a point of egress for the embryo.

The immersed oœcium with the pore which seems sometimes to assume the shape of a small operculum, resembles that of *Cellaria.*

This species is extremely interesting and deserves closer study. It is reported as luxuriant in growth at Houston-Channel, Queen Charlotte Islands. It occurs in small quantity in our collection from Puget Sound, Washington, and from Mendocino City and Pacific Grove, California, where it occurs between tide marks.

Porella Gray.

Cellepora, (part) Fleming, 1828.
Porella Gray, 1848.
Lepralia, Busk, 1854.
Porella, Hincks, 1880.
Porella, Hincks, 1884.

Zoarium incrusting or erect, foliaceous with a single layer of zoœcia, or ramose. *Zoœcia* with the primary orifice semicircular; secondary orifice elongate, inversely subtriangular, or horseshoe-shaped, inclosing an avicularium, usually with a rounded mandible.

This genus is apparently not well represented in this fauna. But one species appears and that is incrusting.

69. **Porella concinna** (Busk) Hincks.

Pl. 22, fig. 65.

Lepralia concinna Busk, 1854, pt. 2, p. 67, pl. 99.
Porella concinna, Hincks, 1880, p. 323, pl. 46.
Porella concinna, Hincks, 1884, vol. 13, p. 50.

Zoarium forming an opaque, white, closely adherent incrustation on stones, shells, etc. *Zoœcia* (pl. 22, fig. 65) ovate, slightly convex, punctate; orifice orbicular, deeply sunk in older zoœcia, with an oval avicularium within or upon its lower margin; immediately below the avicularium, and often hiding it, the zoœcial wall frequently rising into a rounded prominence or mamilla, *mam.;* on each side of the orifice rostra are often formed by a thickening of the wall; frequently a small avicularium, or pore at one side of the mamilla. *Oœcia* small, sparsely punctate, often having an umbo on its front surface

Porella concinna is usually described as having the front wall granular. In his report from the Queen Charlotte Islands, Hincks finds this species punctate as is that occurring in our collection, dredged at 32 fathoms near San Pedro, California.

Escharoides Smitt.

Escharoides Smitt, 1867.
Escharopsis Verrill, 1879.
Escharoides, Hincks, 1880.

Zoarium erect, ramose. *Zoœcia* with primary orifice suborbicular; *peristome* arched above, with a sinus below within which an avicularium is inclosed.

70. **Escharoides sarsi** Smitt.

Pl. 22, figs. 66, 67.

Escharoides Sarsii Smitt, 1867, p. 24, pl. 26, figs. 147-154.
Escharopsis lobata, Verrill, 1879, p. 196.
Escharoides Sarsii, Hincks, 1888, vol. 1, p. 218, pl. 14, fig. 1.

Zoarium partly incrusting, partly forming an erect foliaceous expansion 100 mm. in height, composed of contorted, anastomosing two-layered laminæ. *Zoœcia* elongated, alternate, in the young stage convex, smooth, and perforated round the margin; orifice orbicular, simple (pl. 22, fig. 66); in older stages, as calcification proceeds, the front wall flattens, other pores develop in the new outer layer, fewer and larger ones on the margin appear, and others scattered over the front of the zoœcium (fig. 67); secondary orifice, with a well marked sinus; between these two stages an intermediate stage in which an avicularium is found upon one side of the orifice just within the margin. In older parts of colony this hidden under the thickened calcified crust. *Oœcia?*

A large colony growing over a clam shell obtained at Juneau.

Smittia Hincks.

Berenicia (part) Johnston, 1847.
Lepralia (part) Johnston, 1847.
Lepralia (part), Busk, 1854.
Escharella Smitt, 1873.
Smittia Hincks, 1879.

Zoarium incrusting. *Zoœcia* with the primary orifice suborbicular, the lower margin entire and dentate; peristome elevated and forming a secondary orifice which is channelled in front; generally an *avicularium* below the secondary sinus.

KEY TO SPECIES OF SMITTIA.

1. Front wall porous over the whole surface 2
1. Front wall with marginal pores very marked, frontal pores, if present, few and indistinct 4
2. Avicularia median ..... **S. landsborovi**
2 Avicularia not median 3
3. Avicularia on one or both sides of orifice, sessile ..... **S. trispinosa**
3. Avicularia on one or both sides of orifice, raised on a high mound ..... **S. californiensis**
4. Front wall with prominent processes ..... **S. collifera**
4. Front wall without blunt processes 5
5. Front wall granular, marginal pores large and separated by distinct ribs ..... **S. reticulata**

71. **Smittia trispinosa** (Johnston) Hincks.

Pl. 22, figs. 68, 69, 70.

Lepralia trispinosa Johnston, 1847, ed. 2, p. 324, pl. 57, fig. 7.
Lepralia variolosa Johnston, 1847, ed. 2, p. 317, pl. 55, fig. 8.
Lepralia trispinosa, Busk, 1854, pt. 2, p. 70, pl. 25, figs. 1, 2; pl. 98; pl. 102, fig. 2.
Lepralia trispinosa, Hincks, 1877, vol. 19, p. 100, pl. 11, fig. 1.
Escharella Jacotini, Smitt, 1873, p. 59, pl. 10, figs. 199, 200.
Smittia trispinosa, Hincks, 1880, p. 353, pl. 49, figs. 1-8.

Zoarium forming a rather thick, spiny whitish incrustation on shells, stems of seaweed, etc. (pl. 22, fig. 70). *Zoœcia* elongate-ovate, sometimes quadrangular, in linear series, alternate; front wall convex, granular, punctured round the edge with large pores; similar pores frequently scattered over the surface, though sometimes lacking; primary orifice (fig. 68, *pr. or.*) circular or suborbicular; secondary orifice (fig. 69, *sec. or.*) formed by a high, thin *peristome* possessing a deep sinus, *s.*, within which a denticle, *d.*, is usually visible. In young stages two or three spines (fig. 68, *sp.*) on the upper margin of orifice; spines frequently developed on every zoœcium of the colony. *Avicularia* usually very abundant and very variable in shape and location. Generally one of large size on one side of the orifice, some-

times on both sides; this avicularium (fig. 69, *av.*) may possess a slender triangular mandible directed upward; other smaller *avicularia* frequently scattered over the zoœcia, mandible directed downward, outward, or upward. *Oœcia* large, globose, marked with a few large punctures.

S. trispinosa is reported as abundant at Queen Charlotte Islands. It is a common species in our fauna ranging from Alaska to San Diego, California, from between tide marks to a depth of a few fathoms.

72. **Smittia californiensis** sp. nov.

Pl. 22, fig. 71.

Zoarium forming a thick, coarse, spiny crust of a dark grey color on stems of kelp, shells, etc. *Zoœcia* large, subquadrangular, or rhomboidal on the growing margin of the colony; becoming crowded together, and variously shaped in older portions of the colony; more or less alternate, front wall becoming highly calcified in older stages and having numerous large pores; a row of pores around the margin; below the orifice a convex, granular area (fig. 71, *gra. ar.*) sometimes rising into an umbo with or without an avicularium. Primary orifice orbicular closed by a dark-colored operculum; secondary orifice possessing a well marked sinus, *s.*, on the lower margin within which a denticle is generally found. Four long *spines* on marginal zoœcia, two on intermediate ones. On one side of the orifice, occasionally on both sides, on a mound-like projection is a large *avicularium, av.*, with mandible directed outward or upward; scattered at irregular intervals are many smaller avicularia with mandible directed downward; interspersed between the zoœcia are large *spatulate avicularia, sp. av.*, in size approaching that of a zoœcium and occupying the place of one; mandible large, rounded, and directed upward. *Oœcia?*

S. californiensis possesses many points of resemblance with *S. trispinosa* and perhaps may be regarded as a variant of that cosmopolitan species. It agrees with *S. trispinosa,* var. *munita* Hincks, ('84) in the possession of the elevated avicularia, but in the Victorian form the mandible is directed downward. It also

resembles the variety *spathulata* Smitt ('72), in the possession of the large spatulate avicularia, but in the Floridan species these avicularia occur on the zoœcial wall, not in place of zoœcia as in *S. californiensis.*

The constancy of the characters here enumerated in the diagnosis leads me to regard this as a species peculiar to this coast. It is found at many localities on the southern California coast between tide marks and has been dredged from 13 to 50 fathoms.

73. **Smittia collifera** sp. nov.

Pl. 23, figs. 72, 73.

Zoarium incrusting, at first forming a single layered afterward, a many-layered colony, whose zoœcia become piled up and irregularly arranged. *Zoœcia* ovate, alternate, the front wall of those on the growing edge of the colony, hyaline, margin outlined by a row of large pores, a few large pores scattered over the front wall (pl. 23, fig. 72); in older zoœcia, marginal pores larger, separated by thick calcareous ribs, *rb.* *Orifice* orbicular, at an early stage acquiring a distinct denticle, *d.*, on the lower margin; later, by the growth of a *peristome*, *per.*, a sinus is formed in front within which the median denticle is always visible; minute lateral denticles also present; on the upper margin of the orifice two long *spines*, below the orifice on each side a large, blunt, protuberance, *bl. pro.*, frequently a third appearing between these in the median line. When a blunt protuberance does not develop below the middle of the orifice, an *avicularium* usually found in that situation, with pointed mandible directed upward. If a protuberance does appear, then the avicularium may appear lower on the front wall a little to one side or the other. Sometimes a fourth or even a fifth blunt protuberance present on the front wall and the avicularium may be lacking (fig. 73). *Oœcia*, *oe.*, of moderate size, broader than high and somewhat flattened; front wall possessing a few large pores, and adorned with several protuberances similar to those found on the front wall of the zoœcia.

The remarkable calcareous thickenings which are liberally distributed over the surface of the zoœcia form a very characteristic

feature of this species. In this respect it seems to be allied to *Porella rostrata* Hincks ('80 and '82), an Australian form. The two species differ, however, in the shape and size of the primary orifice and of the ovicells. The Australian species also lacks marginal pores and frontal avicularia.

Smittia collifera was found in considerable abundance growing over a shell. It was dredged off the west coast of Coronados Islands in a depth of 15 to 18 fathoms.

74. **Smittia landsborovi** (Johnston) Hincks.

Pl. 23, fig. 74.

Lepralia Landsborovii Johnston, 1847, p. 310, pl. 54, fig. 9.
Lepralia Landsborovii, Busk, 1854, pl. 86, fig. 1.
Lepralia reticulata, Busk, 1854, p. 66, pl. 102, fig. 1.
Eschara Landsborovii, Alder, 1864, vol. 4, p. 105, pl. 4, figs. 1-3.
Escharella Landsborovii, Smitt, 1873, pt. 2, p. 60, pl. 10, figs. 201, 202.
Smittia Landsborovii, Hincks, 1880, p. 341, pl. 48, figs. 6-9.
Smittia Landsborovii, Hincks, 1888, vol. i, p. 226, pl. 14, fig. 3.

Zoarium incrusting. *Zoœcia* large, ovate, or rhomboidal, elongate, separated by distinct lines, front wall thickly punctured with large pores all over the surface (pl. 23, fig. 74); primary *orifice* circular, secondary *orifice* with high *peristome* channelled in front forming a sinus; just within the sinus a broad median *denticle*, *d.*; small lateral denticles probably present; in front of the median denticle, a sessile *avicularium*, *av.*, with rounded mandible directed downward. *Oœcia* small relatively, closely united with the front wall of the zoœcium against which they lie surrounded by a row of large pores; front wall punctate.

The portion of a colony from which this description is written was not in perfect condition, the orifices being filled with debris so that it is not possible to be sure of the presence of the lateral denticles. The broad denticle is always present. The peristome is high, in older zoœcia, projecting in front of the ovicell when the latter is present. Spatulate avicularia said to be frequently present on one side of the orifice, have not been found.

Smittia landsborovi has been obtained in small quantity near San Pedro, California.

75. **Smittia reticulata** (Macgillivray) Hincks.

Pl. 23, fig. 75, 76.

Lepralia reticulata Macgillivray, 1842, vol. 9, p. 467.
Lepralia reticulata, Johnston, 1847, p. 317, pl. 4, fig. 10.
Lepralia reticulata, Busk, 1854, p. 66, pl. 90, fig. 1; pl. 93, figs. 1-2; pl. 102, fig. 1.
Smittia reticulata, Hincks, 1880, p. 346, pl. 48, fig. 1-5.

Zoarium incrusting. *Zoœcia* ovate-elongate, alternate, strongly areolated round the margins, the calcareous lines separating the areolæ forming rib-like lines extending toward the center of the front wall; front wall granular, somewhat thickened (pl. 23, fig. 75). Primary *orifice* round, secondary *orifice* formed by a thin, high *peristome* channelled in front inclosing a broad median tooth; on each side a smaller triangular tooth; four long delicate spines on the upper margin of the orifice, very conspicuous in the young zoœcia (fig. 76); just below the sinus and slightly elevated, a small rounded *avicularium*. *Oœcia* globose, prominent, adherent to the wall of the upper zoœcium by a strongly calcified rim; wall punctured by a number of pores.

The rounded frontal avicularia relate this species to *S. landsborovi;* its other characters, the reticulated, granular wall, the large oœcium, and the spines on the upper margin of the orifice seem to relate it more closely with the typical *S. reticulata*. Hincks ('80) says that *S. landsborovi* may have a highly calcified state in which the frontal pores disappear and the marginal pores become more prominent, in which case it resembles *S. reticulata* in general appearance. The sculpturing of the wall in our specimens is not due, however, to age since young zoœcia (fig. 76) show it quite as distinctly as older ones. With age the middle portion of the wall, which in youth is thin and hyaline, becomes thicker and more opaque but non-punctate.

Smittia reticulata was found at La Jolla incrusting a holdfast of kelp, and was dredged in ten fathoms off Coronados Islands.

Phylactella Hincks.

Phylactella Hincks, 1879, vol. 3, p. 161.

Zoarium incrusting. *Zoœcia* with primary orifice more or less semicircular, lower margin usually dentate, *peristome* much elevated, rounded in front, entire. No *avicularia*.

76. **Phylactella collaris** Norman.

Pl. 23, fig. 77.

Phylactella collaris Norman, 1866, p. 204.
Phylactella collaris, Hincks, 1880, p. 358, pl. 43, fig. 3.

Zoarium incrusting small pebbles. *Zoœcia* somewhat irregularly arranged, sometimes alternate, sometimes side by side and again without order; depressed proximally, raised distally, punctate. *Orifice* (pl. 23, fig. 77, *pri. or.*) in younger stage, orbicular, with well developed lateral denticles; acquiring a flaring *peristome* which in zoœcia that do not possess an ovicell forms entirely around the primary orifice; more expanded at the sides and in front; in oœcial zoœcia rising in front of the ovicell on each side and forming a frill-like expansion; *peristome* sometimes prolonged downward in the median line into a thickened point, again upturned into a mucro-like projection, *pro.*, which partially hides the large orifice. *Oœcia* thickly punctured, appearing somewhat depressed behind the high peristome.

The species here identified as *Phylactella collaris* Norman is evidently related to that species and yet differs from the description usually given for the type species. The zoœcia of the California specimens are larger than those of the type, and the wall is profusely punctured. According to Hincks ('80), *P. collaris* is subgranular, and in his original description Norman ('66) describes the zoœcia as "granular, not punctured round the margin." A specimen from Plymouth, England, however, dredged at 4 to 25 fathoms, has the front wall distinctly punctured. Evidently this character is a variable one, and the peculiar collar-like expansion of the peristome together with the orbicular primary orifice, in the absence of other distinguishing mark, connects it too closely with the present species to warrant its removal.

Dredged in 45 fathoms on the west coast of the island of Santa Catalina, off the coast of southern California.

Mucronella Hincks.

Berenicia (part) Fleming, 1828.
Lepralia (part) Johnston, 1847.
Lepralia (part), Busk, 1854.
Discopora Smitt, 1867.
Mucronella Hincks, 1880.

Zoarium incrusting. *Zoœcia* with a suborbicular, or semicircular orifice; *peristome* elevated in front into a more or less prominent mucro.

77. **Mucronella pavonella** (Alder) Hincks.

Pl. 23, fig. 78, 79.

Eschara pavonella Alder, 1864, vol. 4, p. 12.
Eschara cribraria Busk, 1856, vol. 4, p. 311, pl. 12, figs. 1-3.
Discopora pavonella, Smitt, 1867, pp. 28 and 178, pl. 27, fig. 181.
Mucronella pavonella, Hincks, 1880, p. 376, pl. 39, figs. 8-10.

Zoarium incrusting, partly free forming two layered undulating, foliaceous expansions. *Zoœcia* large, broadly ovate, alternate, strongly areolated round the margin (pl. 23, fig. 78); margin much thickened, sending thickened ribs between the areolations toward the middle of the front wall; middle portion of front wall thin and slightly roughened; rising into a distinct mucro on the lower margin of the orifice. *Orifice* large, orbicular, without peristome or mucro in younger stage (fig. 79), acquiring a thin, low *peristome* on the upper margin in adult stage (fig. 78). On each side of the orifice an *avicularium* with rounded mandible directed upward. *Oœcia?*

This species is very striking in appearance and may be easily recognized with the naked eye. It has been obtained in small quantity from San Juan Co., Puget Sound. It is reported by Hincks from Queen Charlotte Islands.

78. **Mucronella californica** sp. nov.

Pl. 23, fig. 80.

Zoarium incrusting, forming large, circular colonies of several layers. *Zoœcia* large, ovate, often elongate, in regular lines, alternate, except where layers form one above another when they become irregular in growth. *Primary orifice* circular, *secondary orifice* formed by the growth of a thin *peristome* rising in front on the lower margin of the orifice into a rather broad mucro or tooth; lateral denticles present (pl. 23, fig. 80). A row of pores just inside the margin of each zoœcium and other pores scattered irregularly over the front wall which becomes highly calcified with

age. Three or four small *avicularia* scattered over the surface of each zoœcium, mandible directed transversely or downward. At irregular intervals a large *spatulate avicularium*, *sp. av.*, above or to one side of the orifice, mandible narrowed, curved toward the extremity, and directed obliquely upward. *Oœcia* globose, punctured with a few large pores.

A noticeable feature of this species is the position of the spatulate avicularia which seem by their large size to push the orifice to one side, thus giving it an asymmetrical position (fig. 80, *as. or.*). Zoœcia upon which these large avicularia develop can be recognized at an early stage, where the orifice is asymmetrical before the avicularium is formed.

Mucronella californica is found at several localities on the coast of southern California, and was dredged off the island of Santa Catalina.

Retepora Imperato.

Retepora Imperato, 1572.
Millepora (part) Linnæus, 1766-1768.
Millepora, Pallas, 1766.
Millepora, Ellis, 1767.
Retepora, Johnston, 1847.
Retepora, Lamarck, 1856.
Retepora, Hincks, 1880.

Zoarium adherent by means of an incrusting base, composed in great part of aborted zoœcia. *Zoœcia* disposed on the front surface of an erect, ramose zoarium, whose branches usually anastomose and form a reticulate expansion; *orifice* semicircular and semi-elliptical, with a prominent rostrum on the lower margin bearing an avicularium. *Avicularia* developed on both the dorsal and ventral surfaces of the zoarium.

This genus, according to Hincks ('80), was founded upon the reticulated habit of growth, but since Reteporæ, according to the same writer, occur in which there is no trace of reticulation, too much weight can not be assigned to this peculiar habit. The species of *Retepora* found on this coast, however, assume the reticulate form only (pl. 24, fig. 81). The openings formed by the anastomosing branches are known technically as *fenestræ*, *fen.*, and the sides of the fenestræ are known as *trabeculæ*, *trab.*

79. **Retepora pacifica** sp. nov.

Pl. 24, fig. 81, 82, 83, 84.

Zoarium forming large convoluted masses growing from an incrusting disk, often with a short peduncle (pl. 24, fig. 81). *Fenestræ* oval, about twice as long as wide, on the dorsal surface a much elevated *avicularium* (fig. 82, *d. av.*) at the base of each fenestra, its mandible directed obliquely downward. *Zoœcia* (fig. 83) small, alternate, front wall granular, sloping upward from the sides to the median line. At the growing tip, the young zoœcia (fig. 84), elongate, orifice semicircular on the upper margin, with a notch or sinus on the lower. At each side of the orifice two long *spines,* front wall hyaline. In older stages a high *peristome* (fig. 83, *per.*), with a well defined sinus, below which on most of the older zoœcia there develops a much elevated *avicularium* with pointed mandible directed obliquely downward. *Oœcia* small relatively, set far back, united with the zoœcia only secondarily by the growth of the peristome and perhaps the growth downward of the sides of the oœcium; front wall extremely delicate, usually possessing a distinct denticle, *d.,* on its oral border, curving inward; rarely a spine projecting on each side in front of the oœcium.

Retepora pacifica bears considerable resemblance to *R. Wallichiana,* but differs in some important respects from the description and drawing of that species as furnished by Hincks ('77). *R. Wallichiana* has a rather low peristome and a minute central sinus, while the present species possesses a high, thin peristome with a well marked sinus. The dorsal avicularia in *R. Wallichiana* are small, immersed, with mandible directed transversely; those of *R. pacifica* (fig. 82) are raised, large, its mandible having a distinct downward trend. The shape of the fenestræ is quite different in the two species, those of the present species being twice as long as wide, while those of the specimen of *R. Wallichiana* examined are much more elongated, being five or six times as long as wide. Furthermore, no mention is made of spines on any of the zoœcia of *R. Wallichiana* and they are always readily seen at the young tips of the branches of *R. pacifica.*

The frontal avicularia of *R. pacifica* are not developed on the

lateral zoœcia of the trabeculæ. They are high, *i.e.*, they project from the front of the zoœcia and when viewed in profile resemble the avicularia of the *Bicellariida*. A fine specimen taken at low tide at La Jolla was a deep orange in life. It differs from specimens obtained at higher latitudes mainly in its greater delicacy and in the smaller size of the fenestræ and of the zoœcia. The oœcial wall is extremely thin and the denticle is not always apparent, there being rather a mere tendency to dip downward or slightly inward on the middle of the oral rim.

This species has a wide distribution on the western coast, being found in Puget Sound, San Juan Co., Washington, and at various points on the California coast between tide marks, and dredged from depths of 20 to 30 fathoms.

80. **Retepora pacifica catalinensis** subsp. nov.

Pl. 24, figs. 85, 86.

Dredged on the west coast of the island of Santa Catalina is a quantity of what is considered a variant of *Retepora pacifica*. The zoœcia are smaller than those of the type, but the chief differences lie in the greater height of the peristome and in the loop formed by the peristome in front. The youngest zoœcia at the growing tip cannot be distinguished from those of *R. pacifica* (pl. 24, fig. 84). At an early stage, however, the peristome elevates, especially in front, so that in a zoœcium that has not acquired an ovicell the secondary orifice is almost quadrangular (fig. 85), and instead of a sinus such as appears in *R. pacifica*, a pore, *p.*, is formed by the union of the inner edges of a loop of the peristome, which had they remained apart would have formed a sinus similar to that in *R. pacifica*. In still older zoœcia (fig. 86), the peristome rises still higher into two broad points or plates, *pl.*, which thus form a sinus above the pore. In this stage an avicularium is developed on the front wall of each zoœcium, and an ovicell with a well developed mucro appears. The oœcium, like that of the typical *R. pacifica*, is set far back and thus changes the apparent shape of the secondary orifice. The primary orifice in the sub-species is wholly invisible when the secondary orifice is formed, whereas in *R. pacifica* it (fig. 83, *pri. or.*) may be partially seen even in the oldest stage of growth.

The subsp. *R. pacifica catalinensis* has been obtained in one locality only, dredged on the west coast of the island of Santa Catalina in 45 fathoms.

Celleporidae Hincks.

Celleporidæ (part) Johnston, 1847.
Escharidæ (part) d'Orbigny, 1850-52.
Celleporidæ, Hincks, 1880.

Zoœcia calcareous, more or less vertical to the plane or axis of the colony, irregularly heaped together, with a terminal orifice.

Cellepora (part) Fabricius.

Cellepora Fabricius, 1780.
Millepora, Ellis and Solander, 1786.
Cellepora (part) Johnston, 1847.
Cellepora (part) Lamarck, 1856.
Cellepora, Hincks, 1880.

Zoarium incrusting, often composed of many layers of zoœcia, or erect and ramose. *Zoœcia* urceolate, erect, or suberect, heaped together and irregularly disposed; *orifice* terminal with one or more ascending rostra in connection with it, bearing *avicularia*.

81. **Cellepora incrassata** Lamarck.

Pl. 24, fig. 87, 88.

Cellepora incrassata Lamarck, 1856, ed. 2, vol. 2, p. 256.
Cellepora incrassata, Smitt, 1867, p. 33, figs. 212-216.
Cellepora incrassata, Hincks, 1877, vol. 19, p. 105.
Cellepora incrassata, Robertson, 1900, vol. 2, p. 327.

Zoarium sometimes forming coarse, rounded nodules incrusting seaweed, sometimes rising into thick palmate masses more or less branching. *Zoœcia* large, rotund, decumbent in young colonies becoming erect in older portions of the colony and piled one on top of the other; front wall soon becoming heavily calcified and punctured with large pores (pl. 24, fig. 87). *Primary orifice*, *pri. or.*, rounded on the upper margin with a well pronounced sinus on the lower margin; *secondary orifice* (fig. 88, *sec. or.*) orbicular; on each side an *avicularium* somewhat elevated, the two

often inclined toward each other; mandible directed slightly away from the orifice; avicularia frequently lacking except on zoœcia that bear oœcia. *Oœcia*, *oc.*, small relatively to the size of the zoœcia, recumbent, rounded, smooth, broader than high, a triangular portion, *tri. por.*, in the front which is very transparent and thin, and frequently broken away, thus making the oral arch appear very high.

This species reported from Santa Cruz, California, by Dr. Sinclair (Busk '54), and from Queen Charlotte Islands by Hincks ('84). Our collection shows it obtained at various localities of the more northern coast of California, and also from Alaska.

82. **Cellepora costazi** Audouin.

Pl. 24, fig. 89.

Cellepora Costazii Audouin, 1826.
Cellepora Costazii, Hincks, 1880, p. 411, pl. 55, fig. 11-14.

Zoarium incrusting stems, growing in many superposed layers. *Zoœcia* decumbent, in earliest stages, smooth; in later stages, erect, disposed irregularly and crowded together one on top of another, wall perforated by large pores (pl. 24, fig. 89); *orifice* suborbicular, with a sinus on the lower margin; becoming deeply sunk secondarily by the growth of the *peristome* bearing an erect process on each side of the orifice with a small *avicularium* on its summit; sometimes a third process on the upper margin of those zoœcia that do not bear an ovicell; many zoœcia with no process whatsoever. Scattered irregularly over the colony are large raised *spatulate avicularia*, *sp. av.*, formed in place of a zoœcium, mandible rounded and directed in any direction. *Oœcia* decumbent, rounded, smooth, much broader than high, with an area in front pierced by large openings or pores.

This species differs from the typical *C. Costazii* mainly in the perforations of its walls. This can not be said to be due to the calcification that comes with age since it appears in the youngest zoœcia. In other respects it conforms to the type and until comparison can be made it is retained here. Obtained at various points on the southern shores mainly. It is much less abundant than *C. incrassata.*

Selenariidae Busk.

Selenariadæ Busk, 1854.
Selenariidæ Busk, 1859.
Membraniporidæ (sp.) Smitt, 1873.
Microporidæ (sp.) Smitt, 1873.

Zoarium more or less regularly orbicular, convex on one side, plane or convex on the other, probably free. Furnished with large and powerful *vibracula* (probably locomotive) often having arenaceous particles affixed in the center of the under surface.

The relationship of this family is by no means clear and its insertion in this list following the *Celleporidæ* is not intended to represent its true taxonomic position. As Smitt ('72) maintains there is considerable resemblance between the zoœcia of *Cupularia* and *Membranipora*, and perhaps a closer resemblance between the opercula of *Cupularia* and *Micropora*. No investigations, as far as I know, have been made on living colonies nor on the embryology, or on any part of the development of any member of this family, so that its true relationship is still a matter of doubt. But one species occurs in our collection and all of the specimens obtained, although recent, were dry and more or less worn.

Cupularia Lamouroux.

Cupularia Lamouroux, 1821.
Lunulites Lonsdale, 1845.
Cupularia, Busk, 1854.

Zoarium circular or oval, convex, free. Each zoœcium furnished with a vibracular chamber and a long seta, disposed in alternate rows radiating from the center or apex of the zoarium.

83. **Cupularia canariensis** Busk.

Pl. 24, figs. 90. 91.

Cupularia canariensis Busk, 1859, vol. 7, p. 66, pl. 23, figs. 6-9.
Cupularia canariensis Busk, 1859, p. 87, pl. 13, fig. 2.
Membranipora canariensis, Smitt, 1873, pt. 2, p. 10, pl. 2, figs. 69-71.
Cupulifera (sp.), Arnold, 1903, p. 92.

Zoarium circular in younger stages, afterward becoming somewhat oblong, conical, sometimes very convex on the upper surface, concave on the lower, touching the substratum only on the

rim of the colony (pl. 24, fig. 90); rim crenulated, each crenula occupied by a vibracular chamber with its long seta. *Zoœcia* alternate, oval or rhomdoidal, surface granular, plain; in zoœcia near the growing rim the middle part of the front wall thinner, and outlined by a row of pores (fig. 91, *p.*). *Operculum, op.*, semicircular above, straight below, surrounded by a rather heavy chitinous rim, *chi. r.*, continuous apparently with a similar rim supporting the vibraculum. *Vibracular chamber* at the distal extremity of each zoœcium, large, with a distinct auricular projection on one side; *seta* long, when extended along the groove as long as two zoœcia. *Oœcia?* Dorsal surface marked by sulci or grooves which correspond roughly with the radiating rows of zoœcia.

According to Arnold ('03) this species is quite abundant in the Pleistocene of Dead Man's Island, San Pedro, California. It has also been obtained living at a depth of four fathoms near San Pedro and dredged off the Island of Santa Catalina.

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Berkeley, Cal., August 1, 1906.

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ABBREVIATIONS USED IN THE PLATES.

a.—apex.
ab.—aboral.
add. mus.—adductor muscle.
ang.—angle.
ant.—anterior.
ant. or.—anterior orifice.
ap.—aperture.
ap. t.—apical tuft.
ar.—area.
arc.—areolations.
as. or.—asymmetrical orifice.
av.—avicularium.
av. m.—avicularian mound.
bl. pro.—blunt process.
bl. sp.—blunt spine.
br. sp.—branched spine.
cal. ar.—calcareous area.
cal. lam.—calcareous lamina.
cal. wa.—calcareous wall.
chi. r.—chitinous rim.
cl. m.—cell mass.
d.—denticle.
d. av.—dorsal avicularium.
dis. w.—distal wall.
ep. pro.—epithelial process.
fd. mem.—folded membrane.
fen.—fenestra.
fi.—fiber.
fl. sp.—flaring spine.
flx. sp.—flexible spine.
for.—foramen.
fr. sp.—frontal spine.
gr. r.—growing rim.
gra. ar.—granular area.
in. op.—inner operculum.
int.—intestinal tract.
im. zoe.—immature zoœcia.
k.—keel.
lat. mem.—lateral membrane.
lat. pro.—lateral process.
lat. sp.—lateral spine.
m.—mouth.
man.—mandible.
mam.—mamillary process.
mar.—margin.
mus. att.—muscular attachment.
mu. pro.—mucronate process.
mu.—mucro.
nk.—neck.
o.—oral.
o. rb.—oral rib.
oe.—oœcium.
op.—operculum.
or.—orifice.
ou. op.—outer operculum.
p.—pore.
p. pl.—porous plate.
p. or.—posterior orifice.
pd.—polypide.
per.—peristome.
pl.—plate.
post.—posterior.
pri. or.—primary orifice.
pro.—process.
pro. m.—protoplasmic mass.
pyr.—pyriform body.
rb.—rib.
re. d.—retractile disk.
re. pd.—retracted polypide.
s.—sinus.
se.—seta.
sec. or.—secondary orifice.
sh.—shell.
sp.—spine.
sp. av.—spatulate avicularium.
sp. pro.—spinous process.
stm.—stomach.
st. c.—stiff cilia.
st. sp.—stiff spine.
suc.—sucker.
t. pro.—tubular process.
t. sp.—tall spine.
th. r.—thickened rim.
trab.—trabecula.
tri. por.—triangular portion.
tri. spa.—triangular space.
tu. ft.—tube feet.
tu. pro.—tubular process.
um.—umbo.
um. pro.—umbonate process.
v. ch.—vibracular chamber.
y. zoe.—young zoœcium.
zoe.—zoœcium.

EXPLANATION OF THE PLATES.

All figures made with the aid of a camera lucida except habit sketches.

PLATE 14.

Fig. 1.—*Membranipora circumclathrata* Hincks. A few zoœcia showing spines on the margin of the aperture (*ap.*), and the areolations (*are.*) between the zoœcia. × 50.

Fig. 2.—*M. circumclathrata.* A single zoœcium (*zoe.*) with its spines and areolations, bearing an oœcium (*oe.*) at its distal extremity. The avicularium (*av.*) of the distal zoœcium perched on the summit of the oœcium. × 50.

Fig. 3.—*Membranipora horrida* Hincks. A few zoœcia showing both stiff spines (*st. sp.*) and flexible spines (*flx. sp.*); also the elongated avicularium below the aperture, and the oœcia (*oe.*). × 30.

Fig. 4.—*M. horrida.* One of the large avicularia, the muscular portion representing the transformed zoœcium (*zoe.*) and its contained polypide, the mandible being the enlarged operculum (*op.*). × 30.

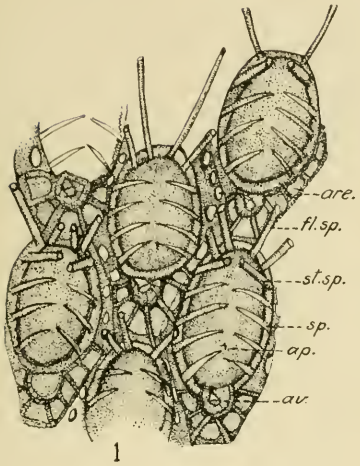
Fig. 5.—*Membranipora lacroixi* Audouin. A few zoœcia showing the granular margin (*mar.*) and the triangular spaces (*tri. spa.*) below the aperture. × 50.

Fig. 6.—*Membranipora occultata* sp. nov. A few zoœcia showing stiff spines (*st. sp.*) and avicularia (*av.*) below the aperture. × 30.

Fig. 7.—*M. occultata.* A few zoœcia showing both stiff and flexible spines (*fl. sp.*), also the oœcia (*oe.*) hidden behind the calcareous wall of the distal zoœcium. × 30.

Fig. 8.—*M. occultata.* One of the large spatulate avicularia. × 30.

Fig. 9.—*M. occultata.* The oœcium (*oc.*) drawn to a larger scale of magnification to show its relation to the calcareous wall (*cal. wa.*) and to the avicularium (*av.*) of the distal zoœcium. × 70.



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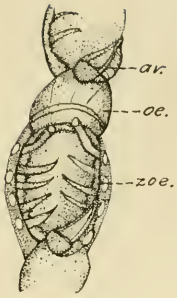

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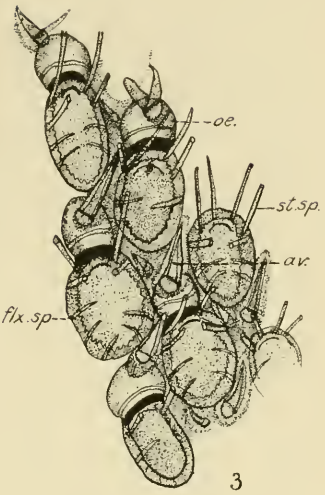

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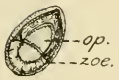

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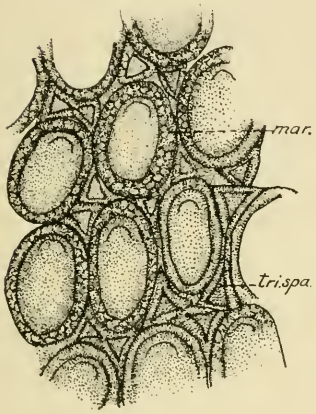

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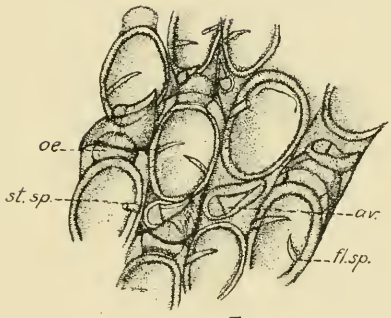

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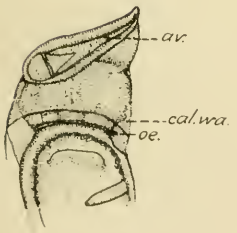

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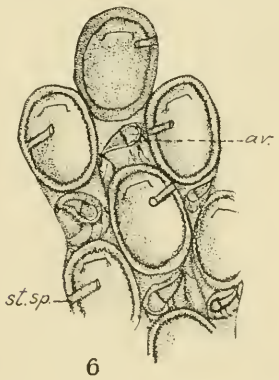

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PLATE 15.

Fig. 10.—*Membranipora patula* Hincks. A few zoœcia showing the broad aperture (*ap.*), spines (*sp.*), the triangular avicularia (*av.*) and the small oœcia (*oe.*). × 30.

Fig. 11.—*Membranipora sandalia* Robertson. A young zoœcium in which the aperture (*ap.*) occupies the whole of the front. × 30.

Fig. 12.—*M. sandalia*. A young zoœcium in which the aperture is reduced in size and is outlined by a circular oral rib (*o. rb.*). × 30.

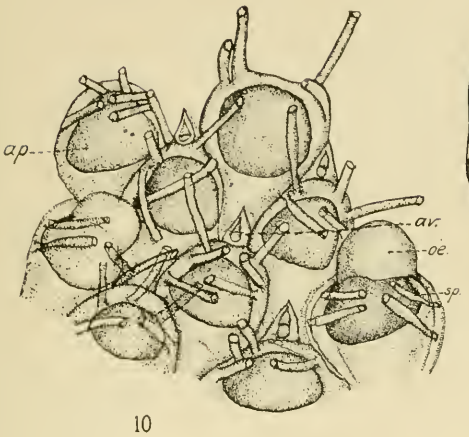
Fig. 13.—*M. sandalia*. A few zoœcia in an intermediate stage of growth showing the calcareous ribs (*rb.*) extending from the lateral margins, and the area (*ar.*) below the orifice where later an avicularium is situated. × 30.

Fig. 14.—*M. sandalia*. A few zoœcia in the adult stage showing the sessile avicularium (*av.*) below the orifice and the calcareous lamina (*cal. lam.*) almost or entirely obscuring the calcareous ribs visible at the stage represented in fig. 13. × 30.

Fig. 15.—*Membranipora spinifera* Johnston. A few zoœcia showing the granular margin beset with spines, and the pedunculated avicularium (*av.*). × 30.

Fig. 16.—*Membranipora tehuelcha* d'Orbigny. A few immature zoœcia and a portion of the growing rim (*gr. r.*). × 30.

Fig. 17.—*M. tehuelcha*. An immature zoœcium showing the beginning of the calcified spines at the distal angles (*ang.*). × 30.



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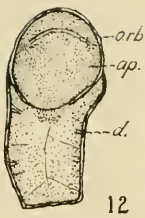

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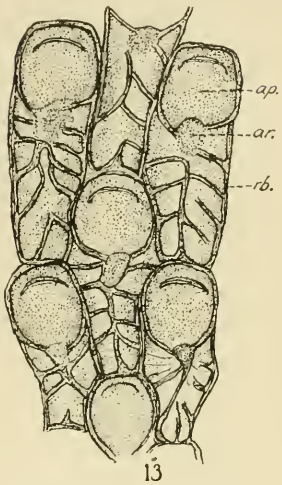

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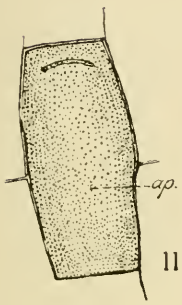

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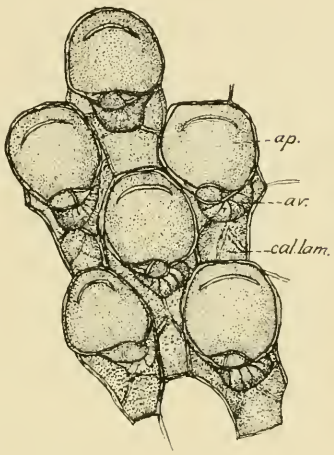

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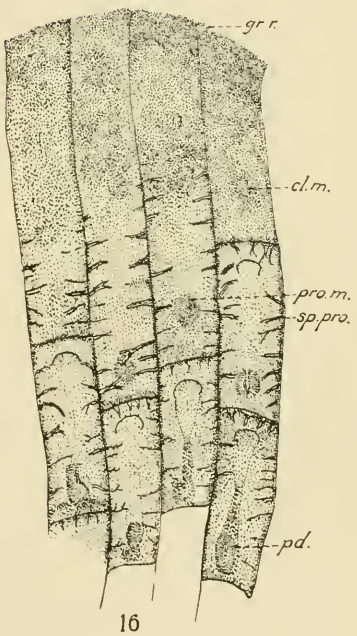

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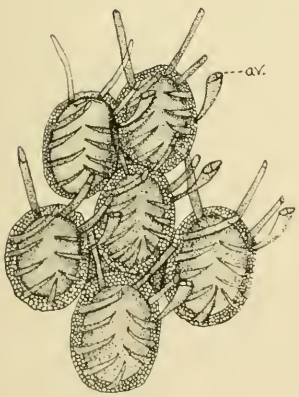

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17

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PLATE 16.

Fig. 18.—*M. tchuelcha*. A few zoœcia showing the adult condition with reduced aperture (*ap.*), calcified margins, and calcareous tubercles or spines (*sp.*). × 30.

Fig. 19.—*Membranipora membranacea* Linnæus. A few zoœcia showing membranous aperture and distal spines. × 30.

Fig. 19a.—*M. membranacea*. Outline of the operculum. × 70.

Fig. 20.—*M. membranacea*. Portion of a zoarium.

Fig. 21.—*Membranipora serrata* Hincks. A few zoœcia showing serrated margin with proximal denticle (*d.*), spines and membranous aperture. × 30.

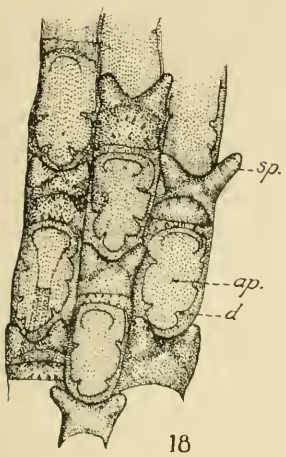
Fig. 21a.—*M. serrata*. Outline of operculum. × 70.

Fig. 22.—*Membranipora villosa* Hincks. A few zoœcia showing adult condition, with flaring spines (*fl. sp.*), lateral spines (*lat. sp.*), and minute frontal spines (*fr. sp.*); also tall spine (*t. sp.*) or process growing in place of a zoœcium. × 30.

Fig. 22a.—*M. villosa*. Outline of operculum when closed, with the most anterior pair of frontal spinules. × 70.

Fig. 22b.—*M. villosa*. Outline of operculum partly opened showing broad base for the attachment of muscles (*mus. att.*). × 70.

Fig. 23.—*M. villosa*. A young colony of seven zoœcia showing (*a*) and (*b*) the first two zoœcia formed, and (*c*) the third zoœcium; also showing the branched spines (*br. sp.*) characteristic of the youthful stage. × 30.



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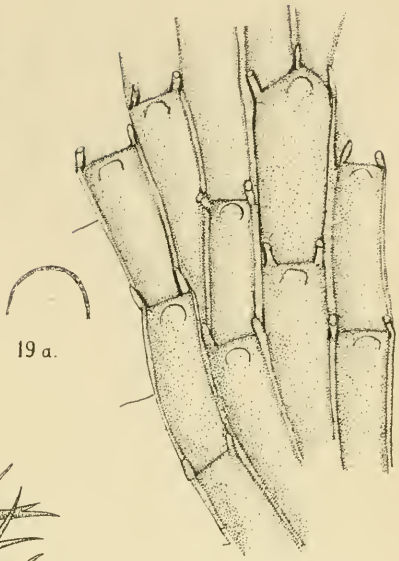

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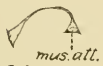

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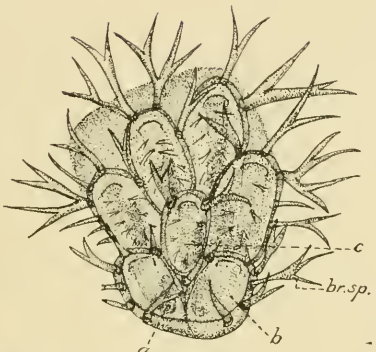

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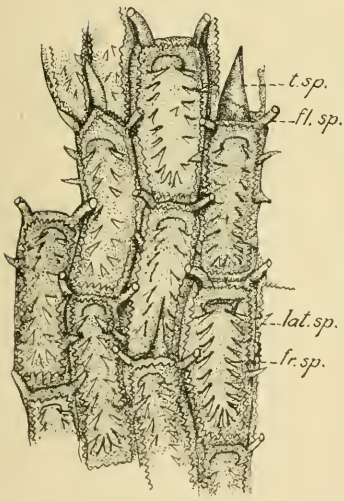

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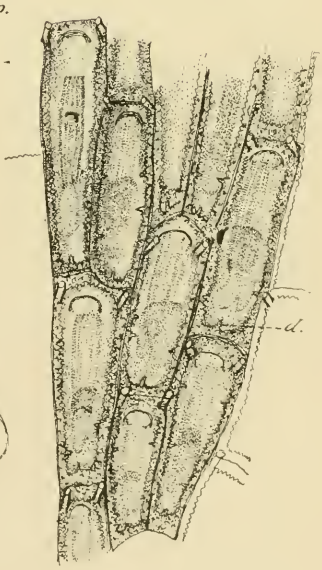

21

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PLATE 17.

Fig. 24.—*Cyphonautes occidentalis* sp. nov. The larval stage of *M. villosa* showing the organism in optical section as it appears while still living and lying on its side. × 70.

Fig. 24a.—*C. occidentalis.* Showing the margin of the first two zoœcia (*a*) and (*b*) through the transparent shell (*sh.*) still adherent to the substratum. × 30.

Fig. 24b.—*M. villosa* Hincks. A young colony of three zoœcia still carrying the shell of the larva. × 30.

Fig. 25.—*M. villosa.* A young colony of five zoœcia. × 30.

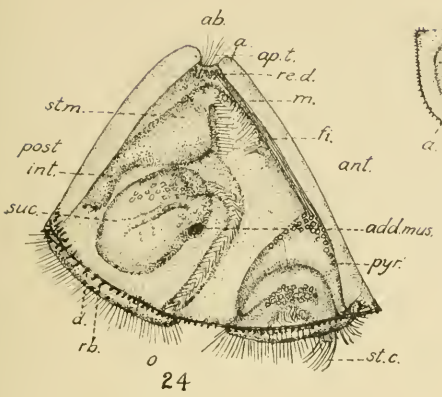
Fig. 26.—*Micropora coriacea* Esper. A few zoœcia showing raised margins, foramina (*for.*) and oœcia (*oe.*). × 30.

Fig. 27a.—*Thalamoporella rozieri* Audouin. Habit sketch of a portion of an incrusting colony. Natural size.

Fig. 27.—*T. rozieri.* Habit sketch of a portion of a branching colony. Natural size.

Fig. 28.—*T. rozieri.* A few zoœcia in the adult condition showing operculum (*op.*) and posterior portion of orifice (*p. or.*); also foramen (*for.*) and blunt process (*bl. pro.*). × 30.

Fig. 29.—*T. rozieri.* Three zoœcia showing great size of the bilobate oœcia (*oe.*) and the diminutive size of the zoœcia bearing them. × 30 .



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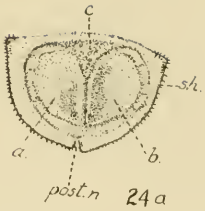

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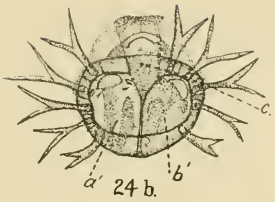

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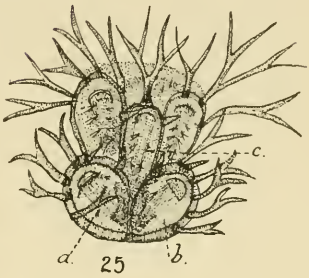

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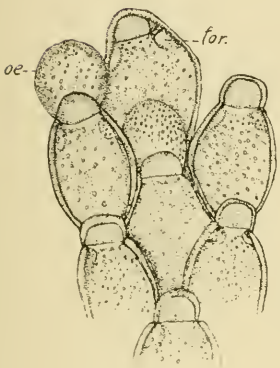

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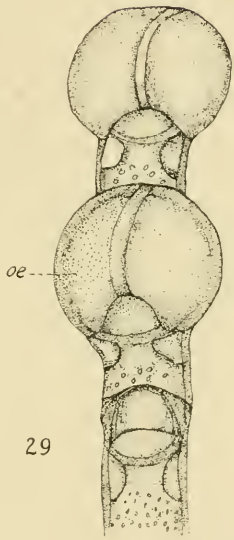

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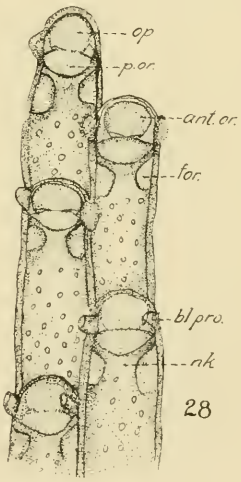

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PLATE 18.

Fig. 30.—*T. rozieri.* A few zoœcia in the adult condition without blunt processes and showing a large spatulate avicularium (*sp. av.*). × 30.

Fig. 31.—*Cribrilina hippocrepis* Hincks. A few adult zoœcia showing arrangement of the perforated furrows, the oœcia (*oc.*), and a large avicularium (*av.*). × 30.

Fig. 32.—*Microporella californica* Busk. Habit sketch.

Fig. 33.—*M. californica.* A few zoœcia showing spines, avicularia, pore (*p.*), and oœcia. × 30.

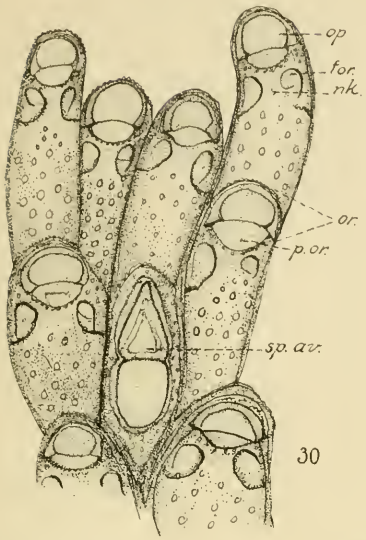
Fig. 34.—*M. californica.* Porous plate which fills in the pore. × 70.

Fig. 35.—*Microporella malusi* Audouin. A few zoœcia showing lunate pore (*p.*), and oœcia (*oc.*). × 30.

Fig. 36.—*M. malusi.* Primary zoœcium showing membranous primary aperture surrounded with spines. × 30.

Fig. 37.—*Lagenipora spinulosa* Hincks. A few zoœcia showing tubular prolongation (*t. pro.*), spines, oœcium (*oc.*), and elevated avicularia (*av.*). × 30.

Fig. 38.—*Schizoporella areolata* Busk. A few zoœcia showing adult condition. × 30.



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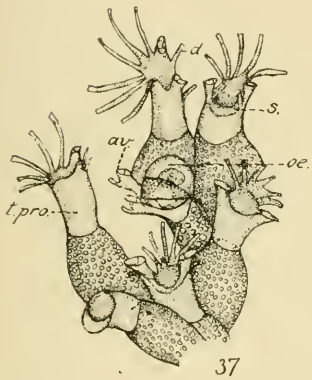

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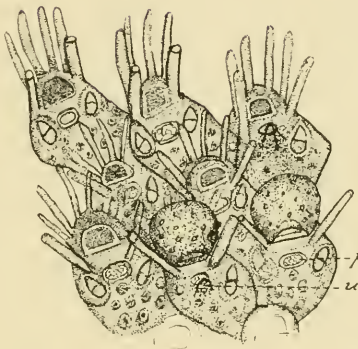

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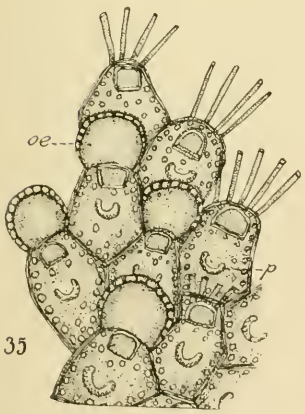

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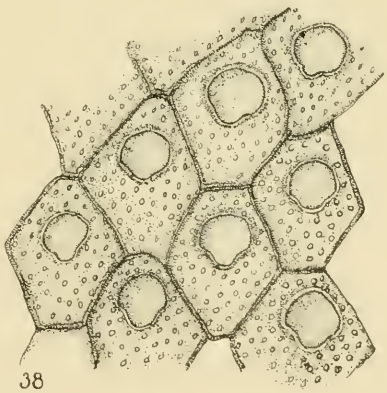

38

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PLATE 19.

Fig. 39.—*Schizoporella auriculata* Hassall. A few zoœcia showing rounded avicularium (*av.*) below the orifice and oœcia (*oe.*). × 30.

Fig. 40.—*Schizoporella auriculata* subsp. *ochracea* Hincks. A few zoœcia showing the elongated avicularium (*av.*) below the orifice. × 30.

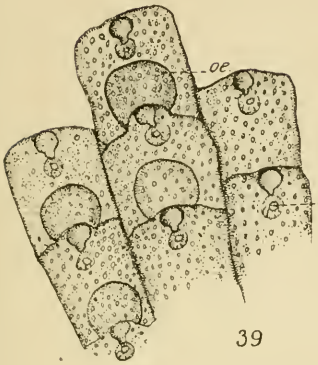
Fig. 41.—*Schizoporella biaperta* Michelin. A few zoœcia showing avicularium on each side of the orifice, also the frontal avicularium (*av.*) and oœcia (*oe.*). × 30.

Fig. 42.—*Schizoporella cecili* Audouin. A few zoœcia showing the characteristic orifice (*or.*) and smooth oœcium (*oe.*). × 30.

Fig. 43.—*Schizoporella hyalina* Linnæus. A few zoœcia showing reticulations between them and the processes on each side of the orifice. × 50.

Fig. 44.—*S. hyalina.* Zoœcia having well marked transverse ridges, an umbo (*um.*) below the sinus, and one on the front wall of the oœcium. × 50.

Fig. 45.—*S. hyalina.* A few zoœcia of the more opaque variety with orbicular orifice and a decided umbo below it (*um.*). × 50.



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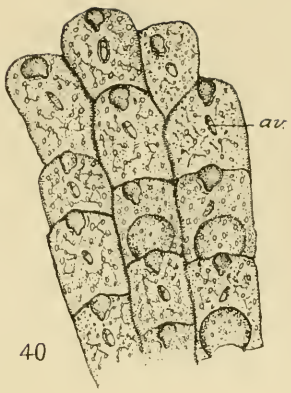

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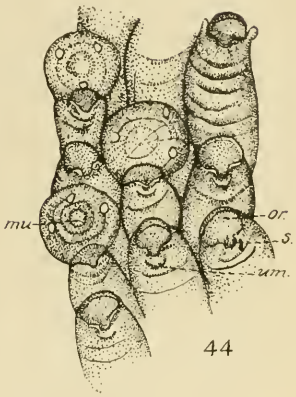

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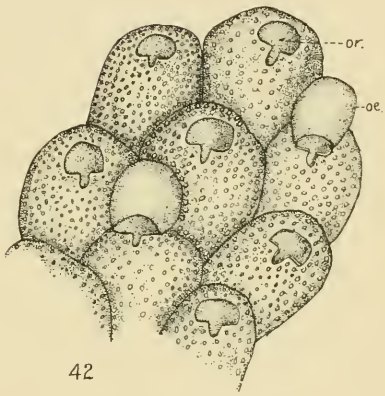

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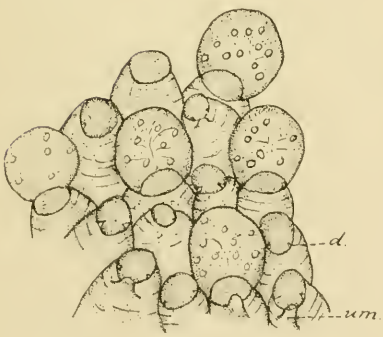

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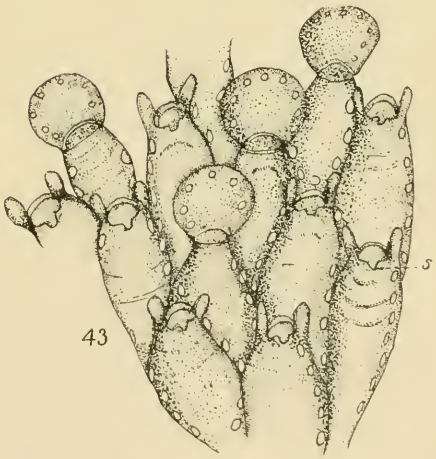

43

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PLATE 20.

Fig. 46.—*Schizoporella insculpta* Hincks. A few zoœcia showing large orifice (*or.*) and wide sinus (*s.*). × 30.

Fig. 47.—*S. insculpta.* A few zoœcia showing large oœcia (*oe.*). × 30.

Fig. 48.—*Schizoporella linearis* Hassall, subsp. *inarmata* Hincks. A few zoœcia without avicularia characteristic of this species. × 30.

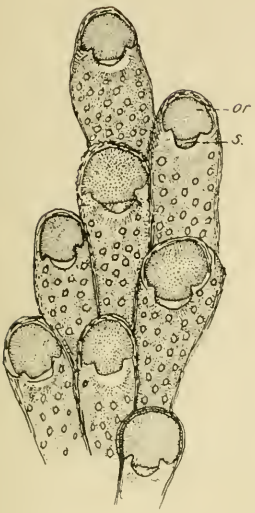
Fig. 49.—*Schizoporella longirostrata* Hincks. A few zoœcia in the adult condition. × 30.

Fig. 50.—*Schizoporella oligopus* sp. nov. The dorsal surface of a few zoœcia showing the calcareous tubular projections or feet (*tu. ft.*) by which this species attaches itself to the substratum. × 30.

Fig. 51.—*S. oligopus.* A few zoœcia in the adult stage showing avicularium (*av.*), the umbo (*um.*) below the orifice, and the foramina (*for.*) between the zoœcia. × 30.

Fig. 52.—*S. oligopus.* A few zoœcia showing the oœcia (*oe.*) with crenulated border. × 30.

Fig. 53.—*Schizoporella tumulosa* Hincks. A few zoœcia near the growing edge showing the elevated avicularium (*av.*) and perforated margins. × 30.



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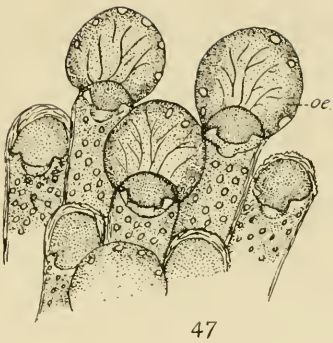

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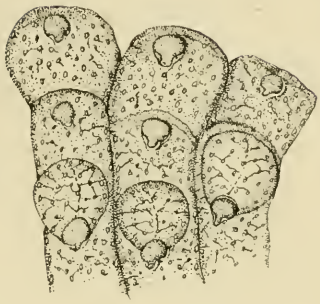

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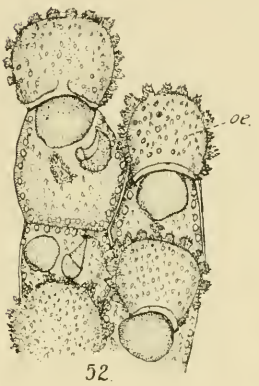

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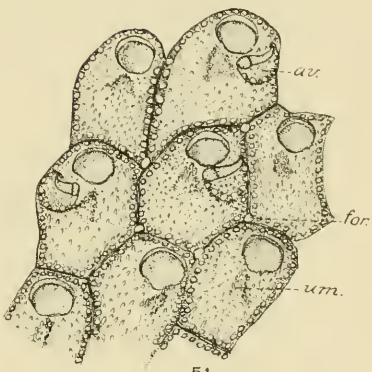

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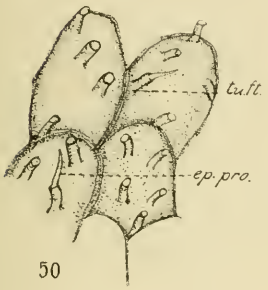

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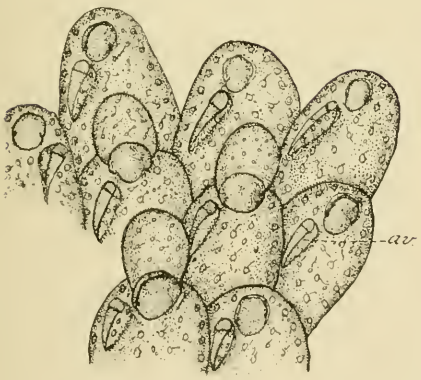

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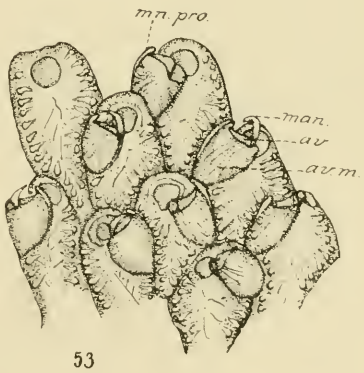

53

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PLATE 21.

Fig. 54.—*Myriozoum crustaceum* Smitt. A few zoœcia showing typical orifice (*or.*), lateral avicularia (*av.*), and oœcia (*oe.*). × 30.

Fig. 55.—*Myriozoum coarctatum* Sars. A few immersed zoœcia. × 30.

Fig. 56.—*M. coarctatum.* Cross section of the stem showing arrangement of zoœcia around the center.

Fig. 57.—*M. coarctatum.* Habit sketch. Natural size.

Fig. 58.—*Myriozoum subgracile* d'Orbigny. A few immersed zoœcia showing avicularium (*av.*) above the orifice. × 30.

Fig. 59.—*Hippothoa divaricata* Lamouroux. Habit sketch. × 8.

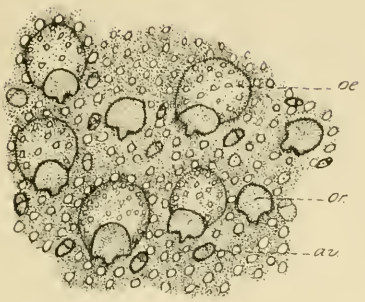
Fig. 60.—*H. divaricata.* A few zoœcia showing median keel (*k.*), and small oœcia on diminutive zoœcia. × 50.

Fig. 61.—*Lepralia bilabiata* Hincks. A few zoœcia at the growing edge of the colony showing the membranous aperture of the immature zoœcia (*im. zoe.*). × 30.

Fig. 62.—*L. bilabiata.* A few adult zoœcia. × 30.

Fig. 63.—*L. bilabiata.* The operculum dissected out.

Fig. 64.—*L. bilabiata.* A single zoœcium with its oœcium (*œ.*) × 30.



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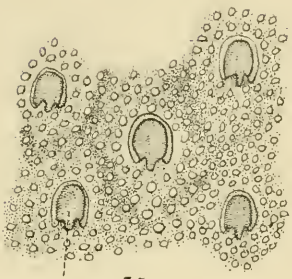

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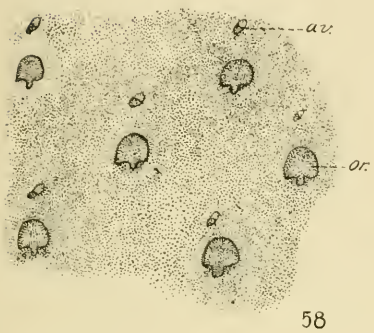
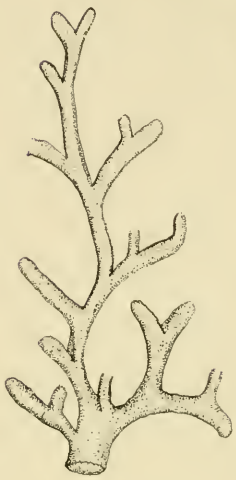


58



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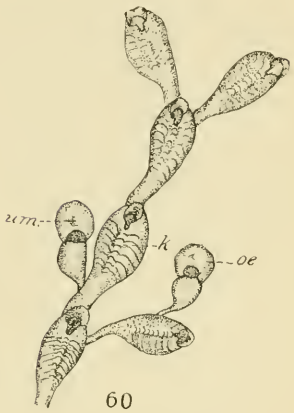

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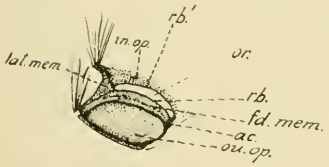

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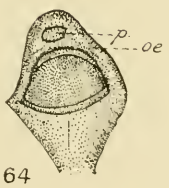

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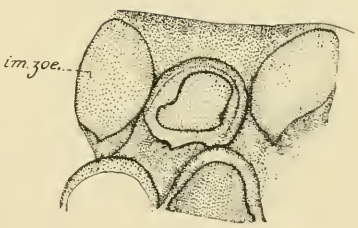

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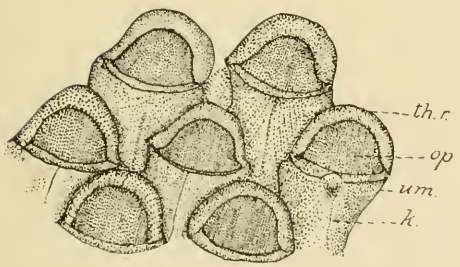

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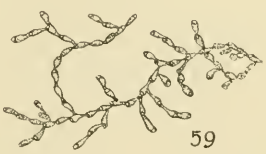

59

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PLATE 22.

Fig. 65.—*Porella concinna* Busk. A few adult zoœcia showing lateral processes (*lat. pro.*), and mamillary process (*mam.*) on the zoœcial and oœcial wall. × 30.

Fig. 66.—*Escharoides sarsi* Smitt. A few young zoœcia showing orbicular orifice (*or.*) smooth, hyaline front wall, perforated inside the margins. × 30.

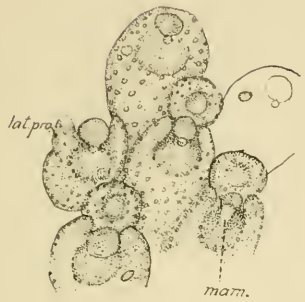
Fig. 67.—*E. sarsi.* A few adult zoœcia, showing orifice with sinus (*s.*) and perforated front wall. × 30.

Fig. 68.—*Smittia trispinosa* Johnston. Three young zoœcia. × 30.

Fig. 69.—*S. trispinosa.* A few adult zoœcia showing perforations of the wall, elongated avicularia (*av.*) and oœcia (*œ*). × 30.

Fig. 70.—*S. trispinosa.* Habit sketch.

Fig. 71.—*Smittia californiensis* sp. nov. A few adult zoœcia showing spines, elevated avicularia (*av.*), and a spatulate avicularium (*sp. av.*).



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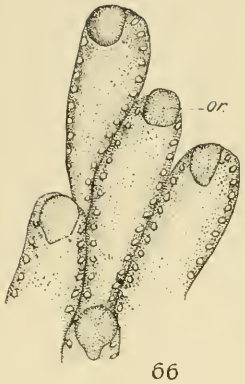

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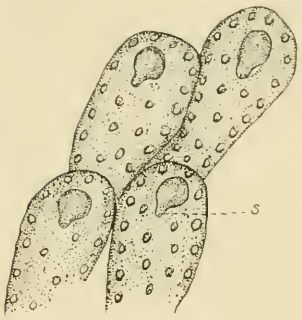

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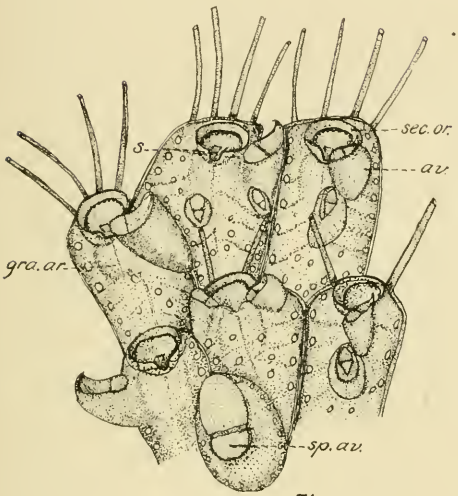

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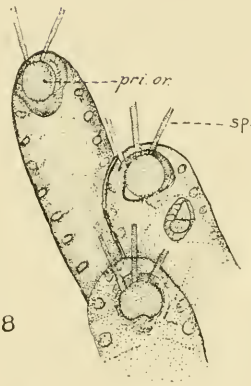

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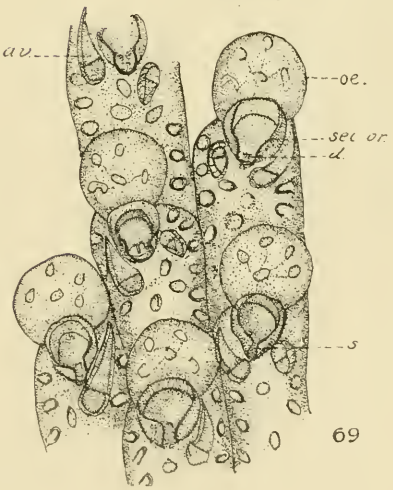

69

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PLATE 23.

Fig. 72.—*Smittia collifera* sp. nov. A few zoœcia near the growing rim showing spines, blunt processes (*bl. pro.*) and avicularia (*av.*). × 30.

Fig. 73.—*S. collifera.* Two adult zoœcia showing increase in number of blunt processes, and an oœcium (*œ.*) ornamented with the same sort of calcareous processes. × 30.

Fig. 74.—*Smittia landsborovi* Johnston. A few adult zoœcia showing porous front wall, rounded avicularium (*av.*), and small oœcia (*œ.*). × 30.

Fig. 75.—*Smittia reticulata* Macgillivray. A few adult zoœcia showing strongly areolated margin, and large oœcia (œ.). × 30.

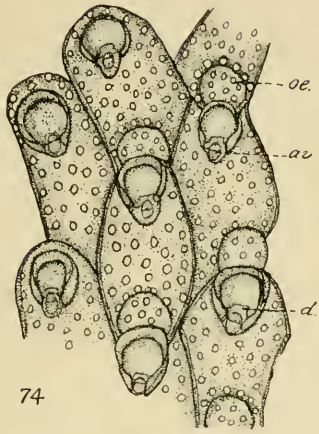
Fig. 76.—*S. reticulata.* A young zoœcium at the growing edge. × 30.

Fig. 77.—*Phylactella collaris* Norman. A few adult zoœcia showing peristome (*per.*) and the frontal process (*pro.*) that sometimes forms on it. × 30.

Fig. 78.—*Mucronella pavonella* Alder. A few adult zoœcia showing large orifice with mucro (*mu.*) on its lower margin. × 30.

Fig. 79.—*M. pavonella.* A young zoœcium at the growing edge showing orifice (*or.*) before mucro has formed. × 30.

Fig. 80.—*Mucronella californica* sp. nov. A few zoœcia showing spatulate avicularia (*sp. av.*) and other avicularia over the surface. × 30.



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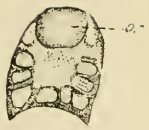

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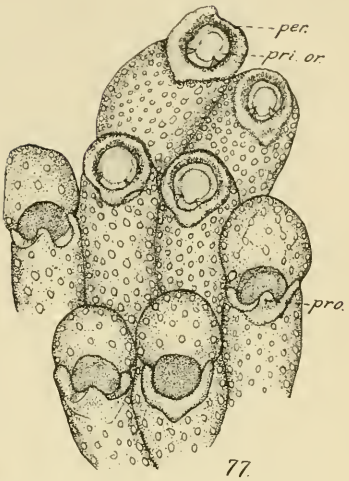

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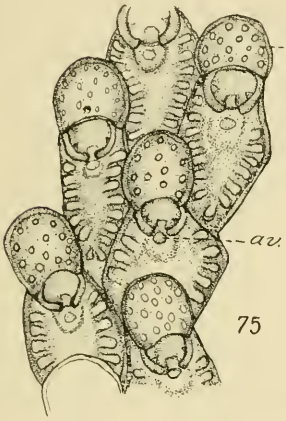

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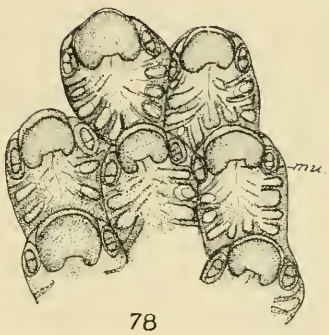

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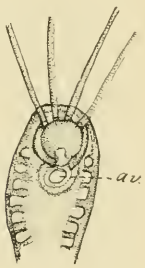
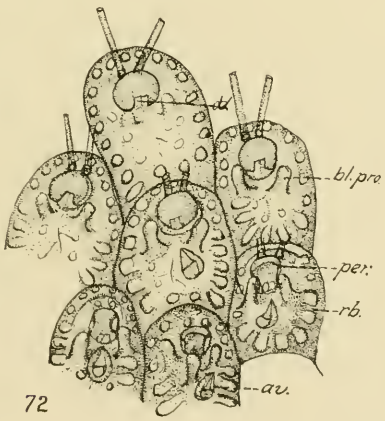


76

73



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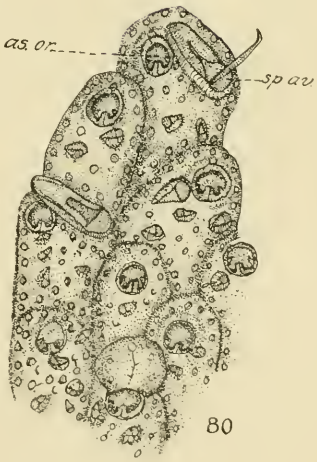

80

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PLATE 24.

Fig. 81.—*Retepora pacifica* sp. nov. Habit sketch.

Fig. 82.—*R. pacifica.* A dorsal avicularium (*d. av.*) at the base of a fenestra (*fen.*). × 50.

Fig. 83.—*R. pacifica.* A few adult zoœcia showing secondary orifice formed by the high peristome (*per.*), elevated frontal avicularium (*av.*) and several oœcium (*oc.*). × 50.

Fig. 84.—*R. pacifica.* A few zoœcia at the growing tip showing primary orifice (*pri. or.*), and spines. × 50.

Fig. 85.—*Retepora pacifica* subsp. *catalinensis* subsp. nov. Portion of a zoœcium to show secondary orifice (*sec. or.*) and pore (*p.*). × 50.

Fig. 86.—*R. pacifica* subsp. *catalinensis.* An adult zoœcium and oœcium. × 50.

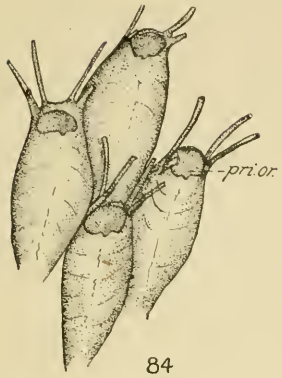
Fig. 87.—*Cellepora incrassata* Lamarck. A few zoœcia showing primary orifice (*pri. or.*). × 50.

Fig. 88.—*C. incrassata.* A few adult zoœcia and oœcia. × 50.

Fig. 89. *Cellepora costazi* Audouin. A few adult zoœcia, oœcia, and spatulate avicularia (*sp. av.*). × 50.

Fig. 90.—*Cupularia canariensis* Busk. Habit sketch of a single colony.

Fig. 91.—*C. canariensis.* A few zoœcia showing the vibracular chambers (*v. ch.*) and long setæ (*sc.*) alternating with the zoœcia. × 30.



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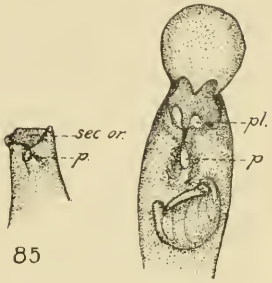

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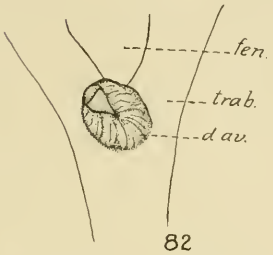

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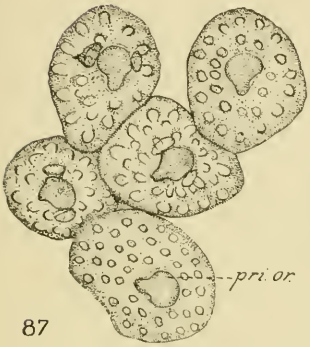

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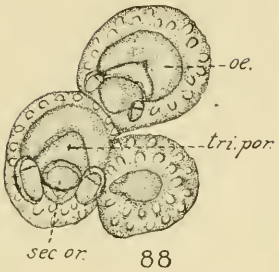

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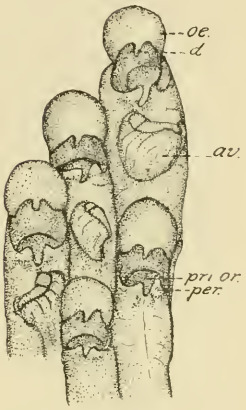

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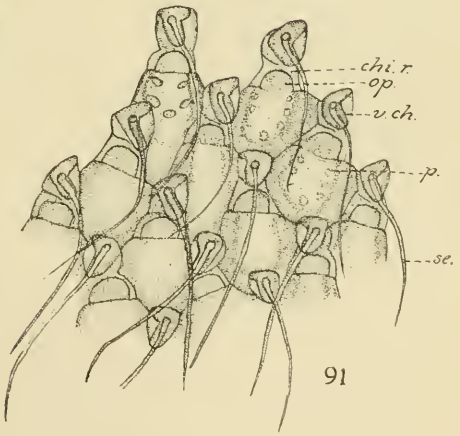

91

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MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO.

XXI.

EXUVIATION, AUTOTOMY AND REGENERATION IN *CERATIUM*.

BY
CHARLES ATWOOD KOFOID.

CONTENTS.

PAGE

Introduction 346
Ecdysis 347
Occurrence in Dinoflagellata 347
Relation to schizogony 348
Exuviation 349
Statement of the problem 349
Structure of the cell wall 349
Transfer of the ancestral theca in schizogony 352
Assimilative regeneration of the theca in schizogony 353
Occurrence of senile forms in *Ceratium* 355
Removal of the wall by solution 356
Evidence of exuviation in *Ceratium* 356
Significance of exuviation 359
Normal autotomy in *Ceratium* 360
Its general occurrence 361
Frequency in collections from deep water 363
Evidence of autotomy 363
Formation of section planes 363
Regulatory character of autotomy 364
Location of planes of autotomy 373
Significance of autotomy 374
Relation to specific gravity 374
Relation to specific surface 374
Regeneration in *Ceratium* 377
After schizogony 377
Regeneration after autotomy 377
Regenerative growth independent of autotomy 379
Regulatory nature of regeneration of the horns 381
Significance of regeneration 381
Summary 383
Bibliography 385

Introduction.

In view of Ostwald's (:03) able discussion of the physical factors of the pelagic environment and Nathanson's (:06) recent suggestive presentation of the phenomenon of vertical circulation in relation to the problems of plankton production, added interest attaches to all structural modifications and adaptations of the organisms constituting the plankton. New meaning and significance appear in characters which have long escaped notice or have been regarded as only additional instances of that wonderful variety of form and wide range of variation within the species which pelagic organisms are wont to exhibit.

In the present paper certain structural features in the skeletal parts of *Ceratium* giving evidence of changes of functional significance are described and these changes are correlated with the problem of flotation as modified by the vertical distribution of temperatures and the possibilities of vertical circulation of oceanic waters.

The genus *Ceratium* is noteworthy among pelagic unicellular organisms for the length and tenuity of the processes or horns which extend from the central midbody containing the nucleus and the main mass of the cytoplasm. In common with the rest of the body they are sheathed within a porulate cellulose wall or exoskeleton. These processes form the single apical and the two (in a few cases, three or more) antapical horns whose position, length, structure and angles of divergence exhibit a most remarkable variety in the scores of species known in the genus. These horns provide, as I have elsewhere (:08) shown, a functional adaptation to flotation and to orientation upon sinking, of prime importance to the species. In the course of my examination of the Dinoflagellates of the plankton of the Pacific off San Diego during the past seven years I have noted numerous instances of individuals with broken horns and many cases of regeneration, in the normal conditions attending the life of the various species in the pelagic habitat. It is the purpose of this paper to discuss these phenomena and the related one of exuviation in normal conditions of pelagic life, and inquire into their significance, es-

pecially with reference to the problem of flotation as affected by the extent and volume of the exoskelton.

The term "ecdysis" or "cytecdysis" will be applied to the process of shedding the entire cell wall at one time and usually in a single piece, in two pieces or in a more or less intact condition. The removal of the wall, plate by plate or in groups of plates of small extent may, on the other hand, be designated as exuviation or cytexuviation. In the first case the cell contents withdraw bodily from the theca, while in the other the cell wall is cast off in parts and with the resulting temporary combination of new and old skeletal parts on one individual.

Ecdysis.

1. *Occurrence in Dinoflagellata.*—In many Dinoflagellates the whole theca is abandoned by the daughter schizonts after schizogony and an entirely new exoskeleton is formed by each of the two or more daughter cells or swarm spores, as for example in *Pyrophacus horologicum* (figs. 1 and 2). At times in those genera in which the parental theca is shed at fission the cell contents may escape from the theca as a *Gymnodinium*-like, naked spore without preceding division, as in *Gonyaulax*, *Diplopsalis* (fig. 3), *Peridinium* (fig. 4) and *Glenodinium*. Subsequently, without intervening division, an entirely new theca is regenerated to replace that lost by this total and simultaneous ecdysis. The thecal plates are usually not dispersed but remain adherent to one another after the escape of the cell contents. Confinement in a crowded plankton collection under conditions of high temperature, more intense illumination than normal and considerable concentration of the products of plant and animal metabolism, induces spontaneously this total simultaneous ecdysis in many Dinoflagellates in the course of several hours after removal from the sea. It also appears to occur normally in the sea to a large extent in *Gonyaulax polyhedra* which forms the patches of "red water" off the coast of Southern California in late summer. In these swarms the numbers of *Gonyaulax* and other Dinoflagellates are so great that the concentration of the products of metabolism must approach that of an ordinary plankton collection, though

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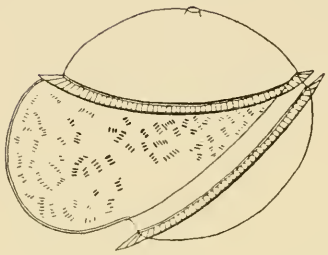

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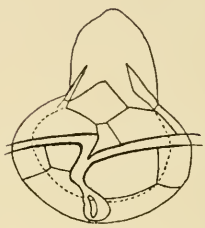

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Fig. 1.—Lateral view of *Pyrophacus horologicum* with swarm spores. × 300. After Schütt ('96).

Fig. 2.—Ventral view of the same after release of swarm spores by opening the girdle suture. × 300. After Schütt ('96).

Fig. 3.—*Diplopsalis lenticula* after treatment with alkali, showing contents escaping through the opened girdle suture. × 430. After Schütt ('95).

Fig. 4.—Ventral view of *Peridinium ovatum* showing spreading of the apical plates and the escape of the cell contents through the apical pore. × 240. After Schütt ('96).

the other environmental conditions such as temperature are not greatly modified. It seems probable that one or more of the changed relations in matters of metabolism brought about by these conditions may induce this total exuviation even in the normal habitat.

2. *Relation to schizogony.*—It is noteworthy that genera which most perfectly exhibit simultaneous ecdysis without attendant schizogony are, in the main, those which at fission and spore formation abandon entirely the parental theca. This is perhaps not a universal rule, for I have found in some species

of *Gonyaulax* unequivocal evidence of *typical oblique fission of the theca* in recent schizonts. In the genus *Ceratium* oblique fission of the theca or exoskeleton universally attends schizogony and the parental theca is shared by the daughter schizonts. Moreover in this genus no instance of *total* ecdysis has been noted in any of the numerous collections of living and preserved plankton which I have examined, neither from the crowded swarms in the "red water" or in condensed plankton collections which have stood in the laboratory for several hours. Fission of the theca in schizogony and entire absence of *total* simultaneous ecdysis thus appear to be the rule in the genus *Ceratium*. The possibility of the occurrence, however, of total ecdysis at the time of sexual reproduction must not be excluded.

Exuviation.

1. *Statement of the problem.*—It becomes, therefore, a matter of interest to consider the formation of the cell wall and the method by which the ancestral theca is passed on in asexual reproduction and what means, if any, exist for ridding the organism of the accumulating products of metabolism found in the cell wall, and of adapting these fixed skeletal structures to the changing environmental conditions which affect profoundly the capacity of the organism for flotation and maintenance in its position within the zone of optimum illumination in the upper levels of the sea.

2. *Structure of the cell wall.*—It is not my purpose to discuss the details of this subject which has been elaborately worked out by Schütt ('95, '99, and :00) but merely to call attention here to the facts pertinent to this discussion. The wall and its superficial modifications are formed of cellulose or of a substance closely allied to it, and the material is laid down on the periphery of the main mass of the cell plasma and its extensions in the apical and antapical horns. Its increase in thickness is brought about probably by appositional rather than intussceptional growth, centripetally on the inner, and centrifugally on the outer face of the wall, but principally by the latter process. Access to the outer face of the wall is gained through the many pores which are distributed in the wall in all regions, though more sparsely towards

the ends of the horns and less abundantly on the thin ventral plate (figs. 5 and 6). The plasma streams out through these pores (Schütt '99) in long filaments and may form an extramembranous sheet on the outer face of the exoskeleton. Both faces

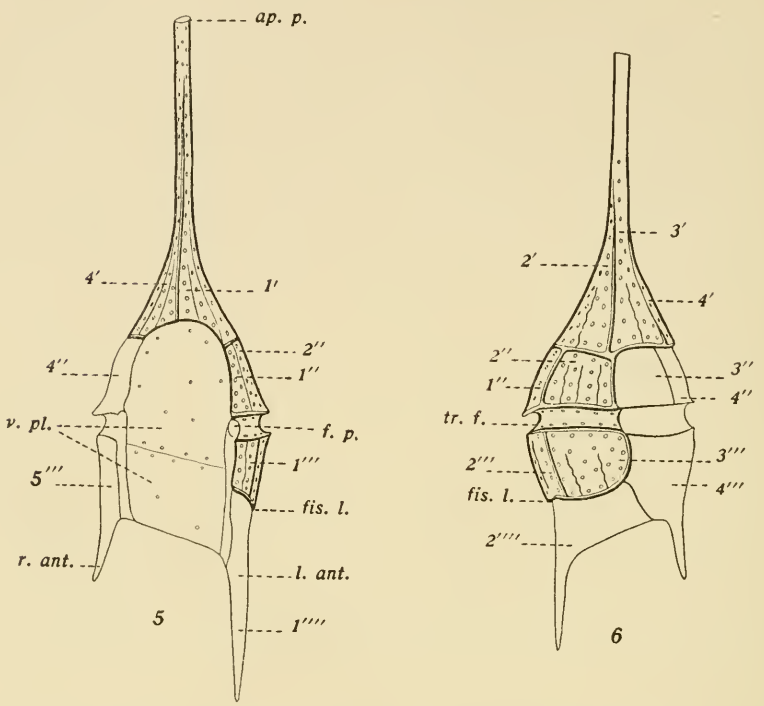


Fig. 5.—Ventral view of *Ceratium eugrammum*, an anterior schizont after recent division. × 913.

Fig. 6.—Dorsal view of the same. Regenerated moiety of the theca shown without pores. × 913.

Abbreviations—*ap. p.*, apical pore; *f. p.*, flagellar pore; *fis. l.*, fission line; *l. ant.*, left antapical; *r. ant.*, right antapical; *tr. f.*, transverse furrow; *v. pl.*, ventral plate; *1′-4′*, apical plates; *1″-4″*, precingular plates; *1′ ″-5′ ″*, postcingular plates; *1″ ″-2″ ″*, antapical plates.

of the cellulose wall are thus accessible to action of the cytoplasm in deposition or solution of the material of the wall.

The thickness of the wall and the extent of its surface differentiations in the form of lists, ribs, fins, and rugosities differ considerably in different species, ranging from the thin hyaline,

structureless, minutely porulate type seen in *C. trichoceros* (fig. 16) to the thick-walled, much ribbed and coarsely porulate one exemplified in *C. robustum* and *C. limulus*. In the normal course of asexual reproduction the type of wall characteristic of the species is maintained by immediate and rapid regeneration of

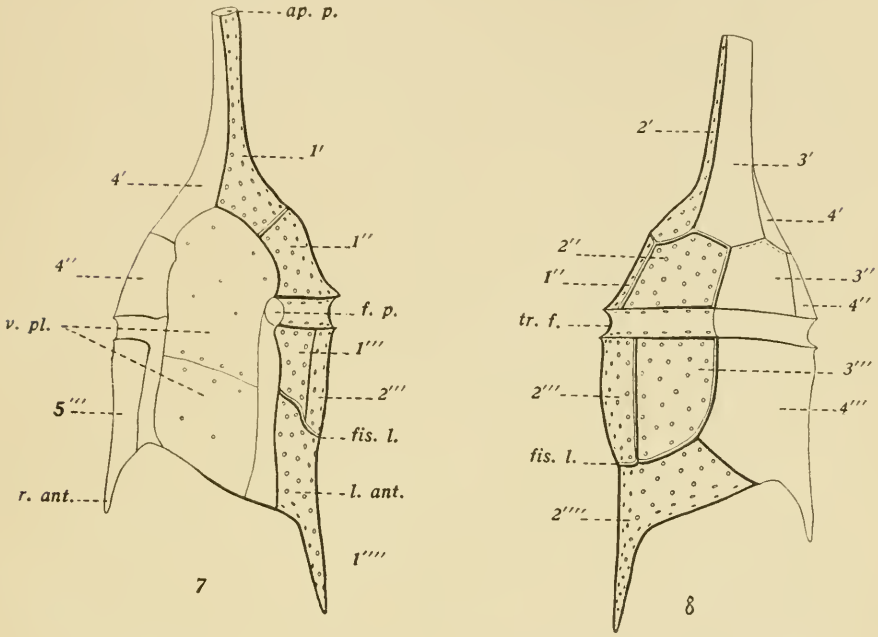


Fig. 7.—Ventral view of another individual after exuviation of part of the thecal plates. Senile theca with heavy sutures and pores. × 880.

Fig. 8.—Dorsal view of same. × 880.

(For explanation of abbreviations, see under figures 5 and 6.)

the new half of each skeleton at the time of schizogony. The differences between the newer and older thecal moieties of individuals recently divided and still in chain are usually obliterated by assimilative regeneration before the separation of the schizonts. On the other hand, within the limits of each species there is a rather wide range of wall structure between the more delicate and the more robust habits, which appears to be correlated with environmental conditions especially those affecting flotation. Occasionally heavily armored individuals of a species are found

whose habit is strongly suggestive of a senile condition and whose cell wall is apparently thickened by the accretions of long-continued growth. Obviously such structure must profoundly affect both metabolism and flotation, for it cuts down the access of light to the chromatophores of the cell on the one hand and on the other affects both specific gravity and specific surface.

3. *Transfer of the ancestral theca in schizogony.*—Asexual reproduction in *Ceratium* as in most Dinoflagellates and the flagellates generally, is accomplished by binary fission, though the

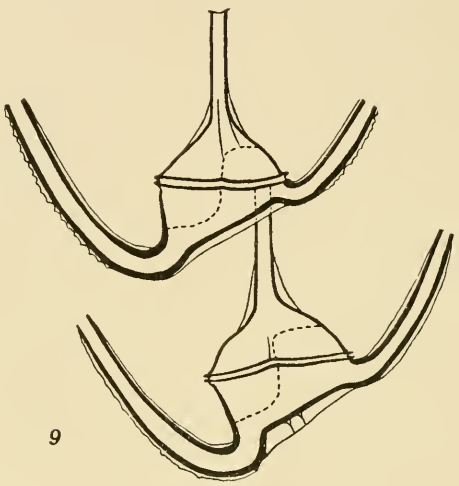


Fig. 9.—Dorsal view of *Ceratium vultur*, a form with short horns in chain showing compensatory character of newly formed thecal moieties, to wit, the two thecal halves between the dotted fission lines. The weight of the lines represents the relative thickness of the walls. × 220.

possibility of multiple spore formation can not be excluded. In the binary fission of *Ceratium*, as has been shown in detail by Lauterborn ('95) for *C. hirundinella*, and as may be seen in most recent schizonts (figs. 5 and 6), the plane of fission is not transverse but passes obliquely across the body from the right anterior to the left posterior margin, separating the parental theca into two parts. The anterior part includes the apical horn and precingular plates 1″ and 2″,[1] and postcingular plates 1′″, 2′″ and 3′″ with the left half of the girdle which is included between the two series of plates. On the dorsal face the suture

line crosses the girdle near the mid-dorsal line (fig. 6) but on the ventral face Lauterborn figures it as passing along the anterior margin of the ventral plate at the base of the apicals and down to the flagellar pore along the right margin of precingular 1′″ and thence through the longitudinal furrow along the right margin of postcingular 1′″ to the postcingular suture. Its course is outlined by a dotted line in figures 4 and 5. The posterior schizont receives the remainder of the plates, precingulars 3″ and 4″, postcingulars 4′″ and 5′″, antapicals 1″″ and 2″″ and the other half of the girdle plates as well as the ventral plate (Lauterborn '95). The right and left antapical horns thus belong to the posterior schizont, and the apical to the anterior one.

At the completion of each schizogony the parental theca is shared in this manner between the two schizonts, each of which regenerates during the process the missing half of the thecal exoskeleton. In chain formation (figs. 9 and 10) which ensues when schizogony is rapidly repeated the two parts of the ancestral theca are found respectively upon the anterior and posterior schizonts of the chain. It is evident that these ancestral portions may continue to form a part of the armor of some two of the offspring for an indefinite time unless some other type of reproduction intervenes, such as spore formation or conjugation, in which the cell contents abandon permanently the thecal exoskeleton of this vegetative period, or unless some modification of the usual physiological processes occurs by virtue of which the thecal wall is resolved or shed in whole or in part.

4. *Assimilative regeneration of the theca in schizogony.*—It might be supposed that these ancestral contributions could be detected readily by their senile characters, such as thickened wall, and excessive development of superficial ribs and lists and increased depth of color, but this does not appear to be the case. In many instances of chain formation which I have observed among various species of this genus I have yet to find an instance in which the older and newer portions of the thecae of the anterior and posterior schizonts of a chain showed any considerable difference in their structural characters suggestive of a senile

[1] I have elsewhere (:07) described the thecal plates of *Ceratium* and proposed the nomenclature here employed.

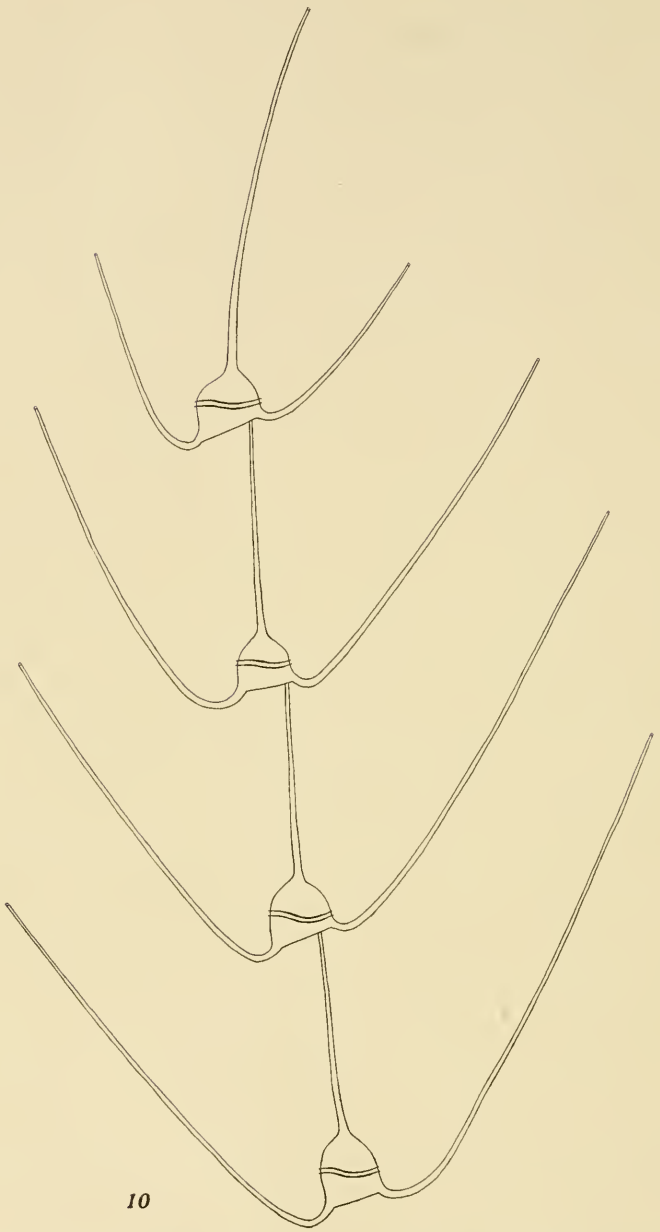


Fig. 10.—Dorsal view of *Ceratium protuberans* (Karsten) in chain. × 100.

condition. This uniformity of skeletal facies is due to the compensatory or assimilative nature of the process of skeletal formation on the newer parts. As a rule a schizont with a rugged, robust, rugose and heavily ribbed ancestral moiety regenerates the lacking part of the thecal wall of a corresponding facies. It is true that schizonts in process of division, or very recently divided, will often have the ancestral portion of the theca upon one side of the fission line of a heavy facies, and upon the other side the recently formed part of more or less delicate habit. Such a condition is, however, temporary and quickly disappears, for it is apparent in the members of a chain of schizonts only in those rare instances where two adjacent individuals have been observed during or immediately after division. The remainder of the chain will be in almost all instances of uniformly rugged or delicate habit (fig. 10) according to the facies of the species or local environmental conditions. Evidence at hand indicates that in marine species chain formation takes place in the course of a few hours in the night. The rapidity of division and of regeneration of the lacking skeletal moiety and the compensatory nature of regeneration serve to obliterate to a large extent the distinctions between the skeletal parts of earlier and later formation. We have in this phenomenon a type of compensatory regulation which preserves in the new individuals the balance of skeletal parts and thus provides for normal locomotion and for orientation by gravity.

5. *Occurrence of senile forms in Ceratium.*—It seems quite probable that long periods of schizogony may prevail in the marine species of this genus. Sexual reproduction and spore formation are, as yet, wholly unknown in any marine forms. Zederbauer (:04 and :04*a*) has observed the former in *C. hirundinella*, a fresh water species, and spore formation among species in that habitat has long been known. If these types of reproduction occur, as they doubtless do, among the marine forms also, they are certainly elusive and possibly rare.

Given a long continued period of schizogony accompanied by some degree of assimilative regeneration of the newly formed portions of the theca in the cases of those schizonts which carry respectively the anterior and posterior moieties of the primal

ancestral theca, we find at once a basis for senility of skeletal parts in *Ceratium*. The origin of this primal theca is as yet unknown, though it may well be supposed to have been formed after an as yet undiscovered (for marine species) phase of sexual reproduction or spore formation in which all parts of prior ancestral thecae were abandoned. It seems probable, therefore, that heavily armored or senile individuals of the various species which are found in any extensive collection of marine plankton owe their origin to the slow accumulation of cellulose on the older thecal moiety and to the accompanying assimilative regeneration which gives a correspondingly rugose or senile aspect to the more recently formed part of the theca, and thus to the whole organism.

It is obvious that the senility here described refers strictly only to the formed skeletal part of ancestral origin and does not apply to the other half of the skeleton or to the cell body. It is therefore a pseudo-senility. Actual senility of the whole organism following upon a long-continued cessation of schizogony has not been detected by me, as such, though detached individuals of senile facies may, indeed, belong to that category.

6. *Removal of wall by solution.*—As before stated, total simultaneous ecdysis which would at once rid the organism of its impeding armor has not been observed in *Ceratium*. Two other possible methods of removal suggest themselves: partial exuviation and the resolution of the wall by the enveloping plasma. No evidence of the latter method has been noted beyond the fact of local solution in autotomy of the horns. Obviously it would be difficult to detect, except by observation during the process. Furthermore, it is probable that if it occurs it would exhibit the same regulatory correlation that is found in thecal formation and result in a reduction of all parts of the theca to a similar type or facies of wall and would, therefore, be difficult to detect.

7. *Evidence of exuviation in Ceratium.*—The removal of the thecal wall by exuviation or progressive shedding of thecal plates has not been hitherto reported. It is, however, easily overlooked and the process may well be more general than the data in hand indicate. Evidence of this method of removal of a greatly thickened ancestral wall, probably at the time of fission in this in-

stanee, is to be found in figures 11 and 12. In a collection of plankton of semitropical contents taken off San Diego in July, 1905, there occurred a *Ceratium arcuatum* (?) which exhibited unequivocal evidence of recent exuviation. As will be seen in the figures the specimen is possibly the anterior schizont of a recent division. The posterior segment of the theca, separated from

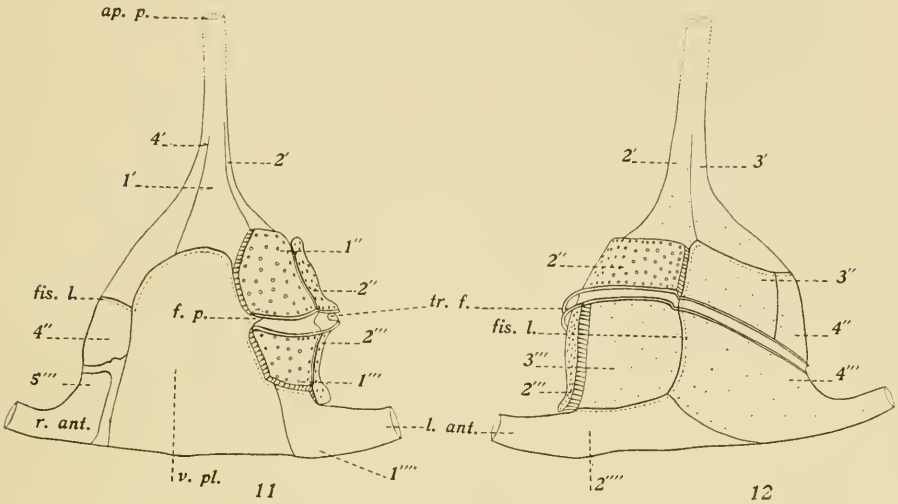


Fig. 11.—Ventral view of *Ceratium arcuatum* (?) in process of exuviation. × 375.

Fig. 12.—Dorsal view of the same. × 375. After sketches by Miss Marie Griffiths.

Specific identification is uncertain in the absence of the complete antapical horns. Precingulars *1″* and *2″* and post-cingulars *1‴* and *2‴* and adjacent girdle are senile plates. The others are all of recent formation.

the anterior by a dotted line in the figures, was very thin-walled and bore all the signs of recent formation. The anterior segment on the other hand had certain plates with strongly marked senile characters while its other plates were of very recent origin, being in fact visible only as exceedingly thin films. The senile plates, four in number, including precingulars 1″ and 2″ and postcingulars 1‴ and 2‴, together with those segments of the girdle plates which go to the anterior schizont in division, were exceedingly thick-walled, with a rugose surface deeply pitted by

well-developed pores. They did not merge gradually into the thin plates upon which they abutted but dropped off abruptly at the suture lines. Their thickness was not less than five times that of the adjacent new plates. The thin-walled plates of the anterior schizont included the four apicals. 1′-4′ and precingulars 3″ and 4″. They were uniformly thin and hyaline and their pores were scarcely visible. The plates of the apical series were least regenerated, and were, indeed, barely formed at the distal end of the apical horn.

The condition of all three horns in this specimen was indicative of their recent autotomy. In *C. arcuatum* in normal condition (fig. 25) the antapicals are much longer than in this specimen and have pointed closed tips. The apical is also normally of at least twice the length in this individual. In this specimen all three horns are abnormally short and the antapicals are abruptly truncated and open. The three horns are, moreover, roughly still in the normal proportions of the horns in *arcuatum* to which species this individual appears to belong. The autotomy of the two antapicals is here attended by a proportionate reduction in the length of the apical.

The conditions here presented by this specimen unquestionably indicate a process of exuviation in which a thecal wall of senile character is in the process of being dropped off plate by plate and replaced by a new wall of delicate texture. The organism does not abandon its old theca as do *Glenodinium* and *Gonyaulax*, but drops it off piece-meal. Of the fifteen main plates of the theca but four here remain of the old type.

It may be significant in this specimen that all four of these plates belong to the *anterior* segment. It is thus possible that this exuviation attended schizogony and that the anterior segment shed its plates and regenerated new ones of a type similar to those forming on the posterior segment as a result of the formation after schizogony of new plates over the whole body, beneath the old on the anterior segment as well as over the posterior segment. The formation of the new plates beneath the old on the anterior moiety would result in the release and falling apart of the superimposed old plates of the anterior segment. It seems probable also that autotomy of the horns of a regulative or com-

pensatory character accompanied or preceded this process of exuviation in this individual.

Another instance of progressive exuviation which is not, however, accompanied by either autotomy or schizogony was noted in *C. eugrammum*, in a collection taken July 1, 1905, from the surface off San Diego. Dorsal and ventral views of this specimen are shown in figures 7 and 8. The right half of the theca is composed of delicate hyaline plates, in which the pores are scarcely visible. The left half, on the other hand, is made up of thick, deeply pitted plates. The line between the two contrasted areas is nearly longitudinal and does not follow the oblique fission line, as will be seen on comparison of the theca of this individual with one after normal fission shown in figures 5 and 6. The heavy portion of the exuviating individual contains most of the plates of the anterior moiety of a recent schizont. It lacks, however, apicals 1′ and 2′ and includes antapicals 1″ ″ and 2″ ″ which belong to the posterior moiety. The hyaline portion of this exuviating individual, which represents approximately the right half of the theca, includes apicals 1′ and 2′ which belong to the anterior moiety and lacks antapicals 1″ ″ and 2″ ″. It seems probable that the senile thecal wall in the right has been exuviated recently and replaced by the new hyaline wall. The distribution of senile plates in both moieties of the theca is conclusive evidence that normal schizogony has not occurred in conjunction with this instance of exuviation, but the possibility of an *abnormally* located fission plane is not necessarily excluded. No instance of abnormally located fission planes has been observed by me in any Dinoflagellate. A number of other instances of partial exuviation were noted in this same collection in *C. gallicum*, *C. inflexum*, and *C. carriense*, and have since been observed by me in these species in other collections.

8. *Significance of exuviation.*—It is obvious that the removal of the heavy senile wall makes possible a restoration of the normal conditions of illumination of the chromatophores and facilitates adjustment of the specific gravity and specific surface to the environmental factors governing flotation. In the collection of plankton in which this exuviating individual was found there was an unusual number of instances of autotomy of the horns in

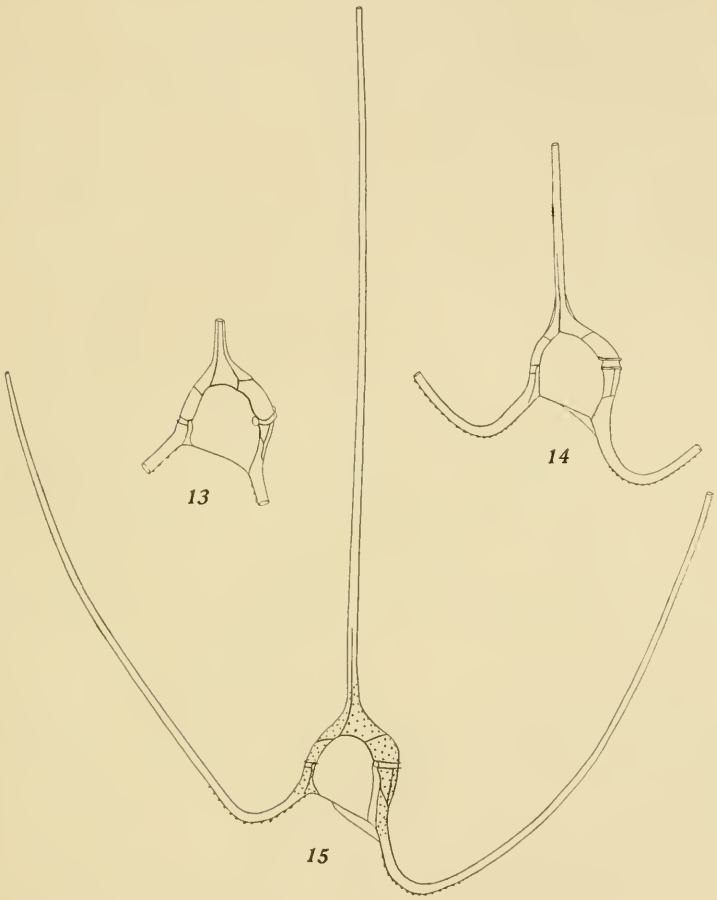
the various species of *Ceratium* represented. The collection had a semi-tropical facies, including such species as *C. trichoceros, C. gallicum* and *C. biceps.* We find in this exuviation an apparent adaptation to changed conditions of flotation. This plankton of semi-tropical aspect may be brought to the San Diego region by occasional invasions of water from the south, possibly by northward extensions of the in-shore counter current which has been reported off Lower California.[2] There is also the possibility that plankton of the warmer surface waters may at times, if not constantly, sink to lower and colder levels. Organisms of the plankton drifting northward or sinking to lower levels are thus brought into regions of lower temperature with increased molecular friction which makes possible a reduction in specific surface. Such a reduction is brought about by the exuviation of the old theca with its lists and rugose surface and its replacement by the smoother new wall, and also by the dropping off of the outer ends of the antapical horns or of all three horns.

Normal Autotomy in Ceratium.

Any observer of marine plankton will have his attention often called to the large number of individuals of *Ceratium*, especially of the longer-horned forms such as *C. biceps,* and many species of the *C. tripos* and *C. macroceros* groups, in which the horns appear to have been broken off. These mutilations are in some cases plainly of the nature of accidental breakages such as might come to pass in the exigencies of life in surface waters or result from collisions and rough handling which these delicate organisms undergo in the course of collection in the plankton net and in subsequent treatment of the material. The frequency with which mutilated individuals were found and especially their abundance in certain collections led me to suspect that other agencies than mere accident were at work in causing this phenomena in most of the mutilated individuals. A careful examination of accumulated data on this point indicates that autotomy of the horns is a normal phenomenon in *Ceratium.* The reasons for this conclusion are as follows:

[2] See Quarterly Current Charts of the Hydrographic Department, British Admiralty ('97).

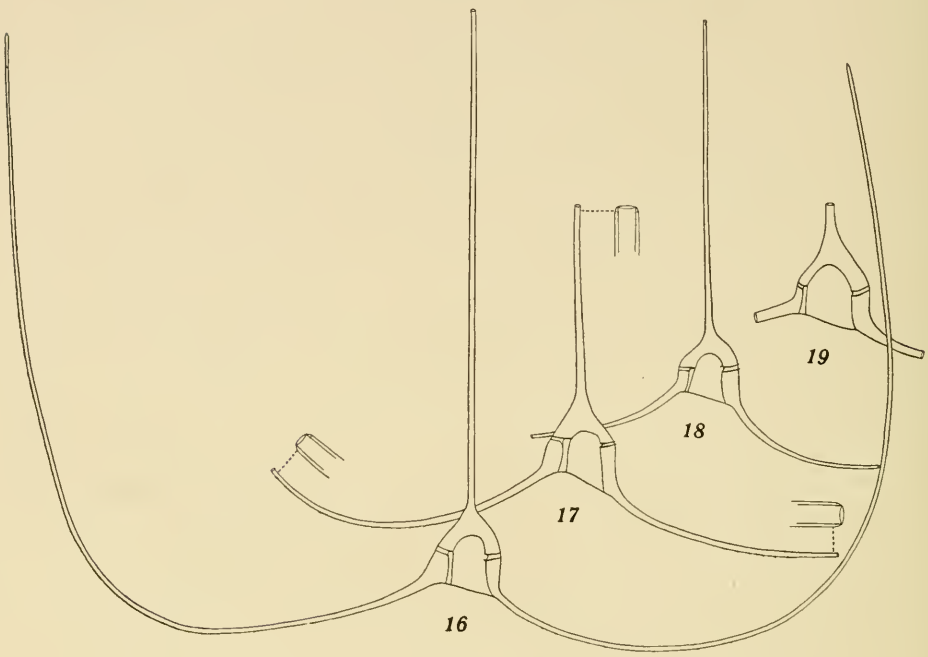
1. *Its general occurrence.*—Few collections from oceanic waters off San Diego in which *Ceratium* is found fail to contain some instances of autotomy. It appears, moreover, in practically all of the long-horned species belonging to the *C. tripos* and *C. macroceros* groups as well as in the more aberrant forms such as *C.*



Figs. 13-15.—Ventral views of *Ceratium gallicum* showing proportionate reduction of the horns in autotomy. × 220.

reticulatum and *C. clavipes.* The examination of a considerable range of collections at San Diego has afforded me evidence that this mutilation is more common in certain species, notably in *C. biceps, C. gallicum* (figs. 13-15) and *C. trichoceros* (figs. 16-19),

and appears occasionally in most of the species having elongated slender horns. I have observed it, for example, in *C. longipes, C. intermedium, C. protuberans* (fig. 20), *C. macroceros, C. ostenfeldi, C. vultur, C. inflexum, C. carriense, C. tripos, C. arcuatum* (figs. 11, 12, 26), *C. schranki, C. azoricum* and *C. hetero-*



Figs. 16-19.—Ventral views of *Ceratium trichoceros* showing progressive and proportionate reduction of the antapical horns in autotomy. × 220. The form of the end of the horns after autotomy is shown under greater magnification in supplementary sketches in connection with figure 17.

camptum. It occurs also in the long-horned members of the subgenus *Amphiceratium* such as *C. extensum* and *C. biceps* (figs. 21-24). It is, however, relatively rare among the species of the subgenus *Biceratium* such as *C. furca, C. lineatum* and *C. eugrammum,* where the antapical horns, and the apical also as a rule, are relatively short and play a less important part in the economy of flotation than they do in the long-horned species of the subgenera *Euceratium* and *Amphiceratium.*

2. *It is more frequently found in collections from deep water* (50-100 fathoms) than in those from the surface. It is also more abundant in collections of tropical facies occurring at San Diego than it is in those made up of species of more northerly distribution. Not infrequently, especially in the winter of 1904, the plankton collections taken off San Diego were unusually rich in species characteristic of the warmer seas, and at such times the proportion of mutilated *Ceratium* was unusually large.

Instances of autotomy of the horns of *Ceratium* occur also in surface collections made off San Diego. There is no evidence at hand to show whether these cases originate in these levels or are brought to the surface by the upwelling of colder water from lower levels a phenomenon known to occur along the California coast (see Holway '06) or by the aspiration of water from lower

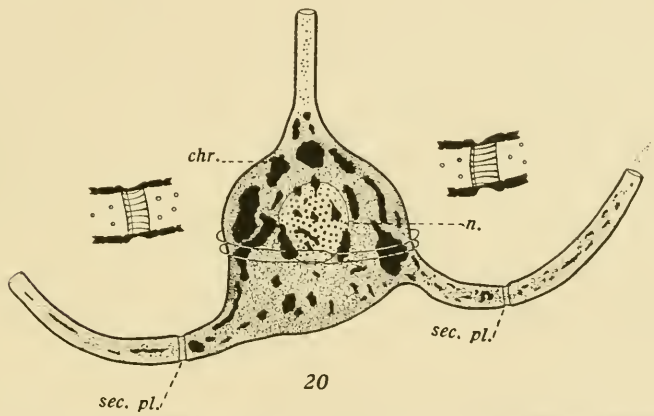


Fig. 20.—Dorsal view (somewhat oblique) of *Ceratium protuberans* in the process of autotomy. × 360. Supplementary sketches indicate the form of the section planes.

Abbreviations—*chr.*, chromatophores; *n.*, nucleus; *sec. pl.*, section plane.

levels in vortices formed between currents of tidal or oceanic nature flowing in opposite directions, as shown by Nathanson ('06).

3. *Evidence of autotomy.*—(*a*) *Formation of section planes.* The horns are cut off by the circular clefts, often though not always quite regular in form and transverse to the axis, which encircle the horns and form (fig. 20) wide V-shaped troughs, wider

at the surface, and steeper on the proximal face, which sink into the substance of the wall and sever it upon all sides. The superficial location of the troughs suggests the agency of the extramembranous plasma in bringing about a local resolution of the cellulose wall. I have found no indications of local solution on the inner face of the wall below the groove. There is no evidence of a withdrawal of the distal plasma from the outer part of the horn to the region proximal to the plane of section in individuals exhibiting the early phases of autotomy. Isolated horns found in the plankton with the proximal stump conforming to the section plane formed by autotomy, often contain a normal plasma core. The line of breakage formed by fracture is, on the other hand, usually an irregular ragged line often oblique to the axis of the horn.

(*b*) *Regulatory character of autotomy.*—One cannot fail to be impressed with the fact that a large proportion of the individuals exhibiting mutilation of the horns have either (1) both antapicals, or (2) all three horns cut off. This appears far in excess of the proportion demanded by the chances of accidental breakage. For example in a collection taken eleven miles off Point Loma on January 12, 1905, from a depth of 60 fathoms, a large number of individuals exhibit mutilation and of the first thirty-five observed in searching material with a mechanical stage no less than twenty-nine had both antapicals cut off, and twenty-six of these also had the apical similarly foreshortened.

The occurrence of individuals in which one or two horns have undergone autotomy while the other two or the third are still in the process is not unusual. An instance of this sort is shown in figure 24 of *C. biceps*, in which the apical is short, possibly as a result of recent autotomy, and the left antapical is nearly severed by two separate and distinct but adjacent section planes at a distance posterior to the girdle approximately proportional to the foreshortened apical horn. Such cases are suggestive of an approximation in the time of the autotomy of the two main horns of this species.

With a view of determining the extent and character of the processes of autotomy and of regeneration in a typical collection from deep water I made an examination of the plankton taken

with a No. 20 silk net, which presumably retains most of the small and short-horned forms of *Ceratium*, from a depth of ninety-six fathoms off San Diego, June 29, 1905. This catch was made by towing at this depth from a drifting boat for about 20 minutes. The net is in action, however, during both the descent to and ascent from this depth. The net presumably obtained a large proportion of its catch from lower levels but also filtered some water from the intervening and surface levels.

Samples withdrawn from the collection were examined with the aid of a mechanical stage and *all individuals of all species of Ceratium* were recorded with reference to their approach to the norm of the species as observed generally in oceanic plankton off San Diego. The length of the horns was measured in transdiameters of the midbody at the girdle of the individual under observation, and the extent of regeneration, if present, was recorded for each of the horns in the same units. By this method the proportionate, compensatory, assimilative or regulatory character of the two processes of autotomy and regeneration of the horns is expressed quantitatively. Since every individual was recorded all elements of personal selection are eliminated.

The results are very striking in that they exhibit the extent to which autotomy and regeneration occurred within the limits between a depth of ninety-six fathoms and the surface and also the degree to which the processes of autotomy and regeneration are regulatory.

The first 125 individuals of Ceratium were recorded as shown in the accompanying table.

Species of Ceratium.

	Normal	Showing autotomy	Showing regeneration	Regeneration without autotomy	Total examined
arcuatum	0	5	0	0	5
axiale	0	1	0	0	1
azoricum	0	4	1	0	4
biceps	8	16	1	1	26
bucephalum	1	0	0	0	1
candelabrum	3	0	0	0	3
carriense	0	2	0	0	2
deflexum	0	1	0	1	2
gallicum	1	6	3	0	7
heterocamptum	2	0	0	0	2
inflexum	1	13	7	2	16
intermedium	1	12	1	0	14
lineatum	5	1	1	0	7
longipes	4	10	3	2	16
macroceros	1	0	0	0	1
protuberans	0	8	0	0	8
seta	1	0	0	0	1
tenuissimum	1	1	1	0	1
teres	1	0	1	0	1
tripos	1	5	0	0	6
vultur	1	0	0	0	1
Total	32	85	19	6	125

These belonged to 21 species, of which 15 were represented in part or wholly by normal individuals, that is by those in which neither autotomy nor regeneration, either with or without preceding autotomy, was evident. In species of the *C. tripos* group autotomy is revealed by the opened tips. In species of the *C. macroceros* group, *carriense*, *deflexum*, *intermedium*, *longipes*, *protuberans*, *tenuissimum* and *vultur*, which normally have open tips, autotomy is only made evident when the arms are appreciably shortened by the process. The detection of individuals in which autotomy had occurred in these species is therefore a matter of judgment and liable to error or prejudice especially in cases approaching the norm of the species. My judgment as to the norm is based upon my impressions after some years of experience in examination of these species and upon the records of many measurements and comparisons with many camera drawings.

But 5 of the 21 species, to wit: *candelabrum, heterocamptum, macroceros, seta* and *vultur* were represented *only* by normal individuals. This is of little significance except in the cases of *C. bucephalum, C. candelabrum, C. heterocamptum* and *C. seta* in which, according to my observations elsewhere, autotomy is relatively rare. It occurs very generally in *C. macroceros* and *C. vultur*. The *total number* of normal individuals was only 32 of the 125 or but 26%, all others showing either autotomy or regeneration or both.

Of the 21 species, 14 or 67% showed autotomy. Those in which it was not recorded being *C. bucephalum, C. candelabrum, C. heterocamptum, C. macroceros, C. seta, C. teres*, and *C. vultur*. It has been seen by me, however, elsewhere in all these species, but is more frequent in those with open tips, *C. macroceros* and *C. vultur*.

Of the 125 individuals 85 or 67% had undergone autotomy, and it was more abundant, moreover, in those species of most frequent occurrence. In the species represented by 4 or more individuals, *C. arcuatum, C. biceps, C. gallicum, C. inflexum, C. intermedium, C. lineatum, C. longipes, C. protuberans*, and *C. tripos*, were included 102 of the 125 individuals. The number of these in which autotomy had occurred was 79, or 77.4%. It is particularly frequent in *C. intermedium* and *C. inflexum*.

Regeneration on the other hand was much less frequent, appearing, after autotomy, in only 19 cases or 15% and without evidence of prior autotomy in but 6 cases or 5%. It is, perhaps, significant that 17 of the 25 instances of regeneration occur in three species *C. gallicum, C. inflexum*, and *C. longipes*, in all of which autotomy is very frequent.

To test the matter of the proportionality of the horns of individuals in which autotomy and regeneration or both have occurred I have taken the first fifty individuals found by the aid of the mechanical stage representing the following species, *C. gallicum, C. inflexum, C. intermedium, C. longipes, C. carriense, C. arcuatum*, and *C. biceps*, merely omitting all normal ones after the first. Measurements of the total lengths of the horns and of their regenerated portions, if any, are given in transdiameters at the girdle in the following table.

Species	Length of horns in transdiameters: Apical	Right	Left	Ratio	Length of regenerated horns in transdiameters: Apical	Right	Left
C. gallicum[2]	4.8	3.8	4.5	1.2	0	0	0
C. gallicum	3.1	1.1	1.7	1.5	0	0	0
C. gallicum	5.4	4.1	5.3	1.3	1.	0.7	0.6
C. gallicum	1.2	1.	1.1	1.1	0	0	0
C. gallicum[1]	7.2	4.5	5.	1.1	0	0	0
C. gallicum	4.6	3.	3.5	1.2	1.	0.6	0.3
C. gallicum	1.2	2.	1.7	0.85	0	0	0
C. gallicum	2.	0.7	1.2	1.7	0	0	0
C. gallicum	1.4	3.7	4.6	1.3	1.2	1.6	1.7
C. inflexum[2]	7.3	6.7	7.9	1.2	0	0.8	0.9
C. inflexum	4.1	3.5	3.3	1.	0.9	1.1	1.2
C. inflexum	5.2	4.6	5.4	1.2	0.7	1.1	1.1
C. inflexum	0.5	1.7	2.2	1.3	0	0	0
C. inflexum[3]	0.9	5.2	6.5	1.2	0	0.3	0.3
C. inflexum[3]	2.9	1.3	4.6	2.5	0	0	0
C. inflexum	4.	3.2	4.3	1.3	0	0.1	0.2
C. inflexum	4.3	3.7	3.8	1.03	0.9	0.9	1.1
C. inflexum	3.8	3.7	3.4	0.9	0	0	0
C. inflexum[3]	0.6	5.7	6.7	1.2	0.6	0.8	1.
C. inflexum	2.6	4.8	4.8	1.	0	1.2	1.
C. inflexum[3]	4.	1.3	3.7[5] 1.7	2.8 1.3			
C. intermedium[2]	3.8	3.2	3.6	1.1	0	0	0
C. intermedium	3.2	2.6	3.3	1.3	0	0.8	0.8
C. intermedium	2.2	2.3	2.4	1.	0	0	0
C. intermedium	1.5	0.5	0.6	1.2	0	0	0
C. intermedium[3]	0.8	1.3	2.4	1.8	0	0	0
C. intermedium	0.5	0.5	0.7	1.2	0	0	0
C. intermedium[3]	5.4	3.8	6.3	1.7	0	0	0
C. intermedium[3]	1.5	0.8	1.4	1.7	0	0	0
C. intermedium	2.3	4.[4] 2.8	3.7	0.9 1.3	0	0	0
C. intermedium[3]	1.8	5.	1.6	0.3	0	0	0
C. intermedium	2.2	1.8	2.3	1.3	0	0	0
C. intermedium	1.	1.5	1.5	1.	0	0	0
C. intermedium	1.	1.1	1.2	1.1	0	0	0
C. longipes[1]	3.	3.	3.	1.	0	0	0
C. longipes[2]	4.5	3.8	4.1	1.1	0.5	0.2	0.3
C. longipes	3.5	1.9	2.8	1.4	0	0	0
C. longipes(1?)	4.	2.5	3.	1.2	0	0	0
C. longipes	0.4	0.3	0.3	1.0	0	0	0
C. longipes	1.2	0.6	0.8	1.3	0	0	0
C. longipes	0.4	0.7	0.8	1.1	0	0	0
C. longipes	1.1	0.6	0.7	1.1	0	0	0
C. longipes	2.	1.4	1.6	1.1	0	0	0
C. longipes[2]	5.5	4.7	5.2	1.1	0.6	0.8	1.1
C. carriense	1.6	1.4	1.7	1.2	0	0	0
C. arcuatum	0.7	0.6	0.8	1.3	0	0	0
C. biceps[1]	23.	0.7	30.	43.	0	0	0
C. biceps	14.1	0.8	11.1	14.	0	0	0
C. biceps	19.	0.8	10.5	13.	0	0	0
C. biceps	4.5	0.5	4.5	9.	0	0	0
C. biceps	3.	0.5	2.5	5.	0	0	0

[1] Normal. [2] Regeneration without indication of autotomy. [3] Autotomy not regulatory. [4] Two section planes at about 2.8. [5] Three section planes at about 1.7.

An examination of the details of this table brings out certain significant tendencies. These appear perhaps most clearly in *C. gallicum*. A presumably normal individual has the apical, right and left antapicals in the ratios of 4.8—3.8—4.5, in a second case 7.2—4.5—5.0. In the six cases of autotomy recorded the apical retains an excess in length in all but two instances and in both of these there was evidence of recent schizogony and active growth of the newly formed apical. It is also noticeable that in four cases a considerable shortening of the apical is attended by much foreshortened antapicals. In the two normal individuals included in the table the relative lengths of the right and left antapical are 1 to 1.2 and 1 to 1.1 respectively. The average for all records of this species in the tables is 1 to 1.25 and for the six which have undergone autotomy 1 to 1.27 (range .85 to 1.7). In all but one instance after autotomy or regeneration or both, the individuals of *C. gallicum* recorded in this table show the left horn slightly longer than the right. These processes are thus regulatory and tend to preserve the norm of the species.

An examination of the data of *C. inflexum* yields somewhat similar conclusions. There are three instances (5, 6 and 10 of the list) in which the apical is noticeably disproportionate. One at least of these (10) is due to recent schizogony. In the other nine cases there is a tendency for a short apical to accompany short antapicals. In all but two instances (2 and 9) the left horn exceeds or equals the right in length, as in *C. gallicum*, and in about the same ratios, averaging 1.26 (or omitting the aberrant 6 the average becomes 1.15). The normal relation of longer left and shorter right horn thus prevails in all but two cases of the twelve. One of the two instances (12) of disproportionately long right horn presents significantly no less than three incipient section planes forming in the longer right horn at about 1.7 transdiameters from the midbody. The completion of this incipient autotomy would bring the ratio of the antapicals to 1.3, nearly the norm for the species. The other case (6) of disproportionate length of antapicals shows not the least trace of approaching regulatory autotomy. In both of these the deficiency of the left horn is slight. The ratio of the two horns after autotomy is in general thus approximately the same as that

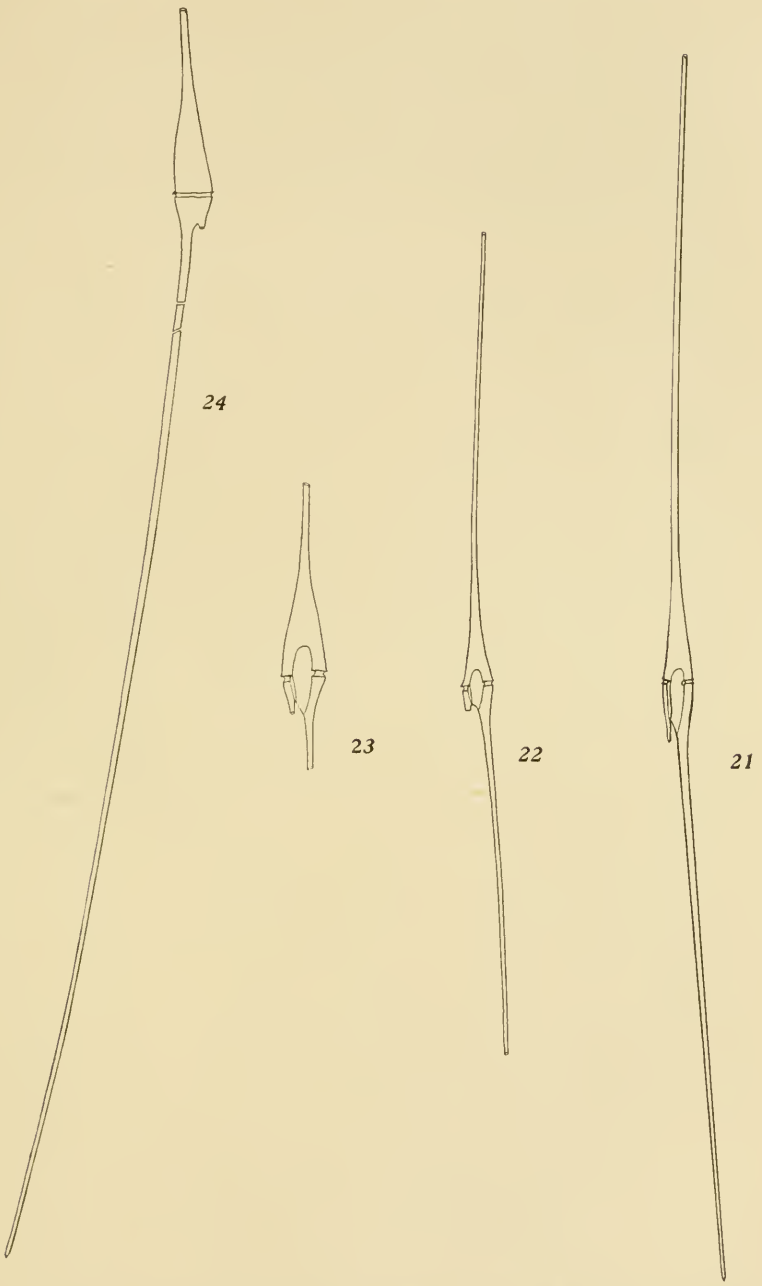
before the process. The first individual listed presents approximately normal conditions and has an antapical ratio of 1.2. With two exceptions in the table the ratios after autotomy lie between 1 and 1.3 or including the two cases of short left horns, between 0.9 and 1.3. The two exceptions both have disproportionately long left horns, that is the right horn has undergone autotomy while the left retains its primitive length.

In the main the data from *C. inflexum* support the view that both autotomy and regeneration are regulatory in this species. The exceptions are such as might attend schizogony or slight departures from coincident autotomy of the horns.

The data from *C. intermedium* are of similar import though somewhat more aberrant. In the thirteen instances there are five (5, 7, 8, 9 and 10) marked cases of disproportionate horns, that is of non-regulatory or possibly partially completed autotomy. One of these (9) has already two section planes at 2.8 transdiameters which when completed would bring the antapical ratio to 1.3, approximately the norm of the species. The remaining eight cases present antapical ratios, after autotomy ranging from 1 to 1.3.

In ten individuals of *C. longipes* there occurred seven instances of autotomy, all of which leave antapical ratios which fall within the limits 1.0 and 1.4, and five of them within 1.0 and 1.2. Similar regulatory relations in autotomy of the antapicals exist in the single individuals of *C. carriense* and *C. arcuatum* which are recorded in the table.

In *C. biceps* the right horn is always relatively very small and plays but little part in the mass relations and form resistance which control orientation and locomotion. Its autotomy and regeneration are, however, of frequent occurrence but are, it seems, often independent of these processes in the other horns. Autotomy of this horn is very frequent, much more so than that of the other horns. In many collections most of the individuals of this species will have the right horn truncated, as though there had been autotomy and subsequent healing without regenerative extension to the slender tapering antapex of typical form. Normal regeneration is, however, occasionally seen. As in other species so also in *C. biceps* there is a correlation in the autotomy



Figs. 21-23.—Ventral views of *Ceratium biceps* showing progressive and proportionate reduction in the apical and left antapical by autotomy. × 100.

Fig. 24.—Ventral view of *Ceratium biceps* after autotomy of the apical horn, showing two section planes, one of which is oblique, forming near the base of the left antapical. × 100.

of the horns. It is most apparent in the tendency toward a proportionate reduction of the large apical at the same time with the left antapical in autotomy. A very short apical is usually accompanied by a very short left antapical. The ratios of the antapicals of *C. biceps*, owing to their normal disproportion, are subject to extreme variations (figs. 21-24) in comparison with those in species having two large antapicals, as shown in the table.

The process of autotomy is thus of normal occurrence to a considerable extent in deep waters in a large number of species of *Ceratium* and is regulatory in character in the main.

Not only is autotomy found concidently, as a rule, in both antapicals, but it usually preserves approximately their relative lengths. As I have elsewhere shown (:07) the right antapical is formed by plates 4′ ″ and 5′ ″ of the postcingular series, while the left is formed entirely by the two plates of the more distal antapical series. This fact lies at the basis of the general occurrence in many of the species of *Ceratium* of an inequality in the length of the antapicals. The right is usually shorter and its base is always nearer the girdle, while the left is longer and its base is farther removed giving to the organism a fundamental asymmetry. This disproportion of the antapicals is most apparent in the subgenus *Biceratium*, while in many species of the *C. macroceros* group the horns are approximately equal, the inequality appearing only on careful measurement. In a few cases in the *C. tripos* group the right horn is the longer one, as frequently in *C. schranki*, and sometimes in *C. arcuatum*.

These sustained proportions in the length of the two horns, and not infrequently in that of all the horns, are characteristic of the species and *they are preserved in autotomy*. An illustration of this appears in *C. gallicum* (figs. 13-15), *C. trichoceros* (figs. 16-19), and *C. biceps* (figs. 21-24), of normal individuals and others which have recently undergone autotomy. The orientation of the organism in flotation and in locomotion is obviously profoundly affected by its form and proportions. The preservation of the fundamental inequality of the antapical horns in autotomy is thus regulatory in character and may indeed be con-

trolled by factors analogous to, or the same as those that determine the original inequality of the antapicals at the time of schizogony. The nucleus is often found near the flagellar pore to the left of the center of the midbody and thus nearer to the base of the longer left horn than to that of the shorter right one. The radius of nuclear activity may be one of the factors influencing the inequality both in growth of the horns and in their subsequent autotomy and regeneration.

A striking instance of this regulatory phase of autotomy of the antapicals appears in those species of *Ceratium* such as *C. schranki* in which the proportionate lengths of the antapicals are reversed, that is the right horn is the longer and the left is normally the shorter one. *This reversal of proportions is usually retained in these species after autotomy.*

In *C. trichoceros* the two horns are nearly equal and vary considerably so that either horn may be the longer. In figures 16 to 19 are shown respectively a normal individual and several after autotomy, in all of which the proportions of the antapicals are approximately maintained. The apical is also shortened by autotomy but the proportion of the horn removed is less than that dropped from the antapicals, and the ratios which the stump bears to the antapicals are less regular than those between the two antapicals themselves. The following table gives the lengths of the three horns:

Ceratium trichoceros, length of horns in transdiameters.

	Apical from girdle	right	left
Fig. 16	8.4	14.	13.7
Fig. 17	3.	4.55	4.65
Fig. 18	5.8	2.6	2.7
Fig. 19	1.25	.65	1.

The location of the planes of autotomy is not a fixed one. Indeed, autotomy may be repeated in the same organism at levels successively nearer the base of the horns (figs. 20 and 24). It is found in different individuals at all levels from the very tip to the base of the horns. A series showing different levels at which autotomy occurs in *C. trichoceros* is found in figures 16 to 19, for *C. gallicum* in figures 13-15, and for *C. biceps* in figures 21-23. A much more complete series might be made for these or many

other species in which autotomy is prevalent. There is no universal or general tendency for autotomy to occur at any particular point. Autotomy in, or near the region of major flexure of the posterior horns is in some of my material more frequent than that in other regions, but there is no definite zone of autotomy here. This wide range in levels at which autotomy appears is in itself strongly indicative that the autotomy is not due to an internal localized structural weakness which renders the arms prone to break at given points, nor to mechanical strains of external origin resulting from impact and producing localized breakage of the arms as a result of the general form of the organism.

Autotomy does not always occur in both antapicals, or in all three horns, coincidently, nor does it always preserve the relative lengths of the horns characteristic of the species, but the proportion of instances in which these phases of the process are not evident is so small that they fall into the category of exceptions to a more general rule.

4. *Significance of autotomy.*—The wide-spread occurrence of this phenomenon is suggestive that it is a normal physiological process subject to regulation in common with growth and regeneration. It is obvious that the loss of the horns modifies the *specific gravity* of the organism only in the event of *unequal* distribution of density of the thecal wall. Evidence upon this point is only indirect. The horns are usually thinner-walled than the midbody, especially in their distal portions. Empty thecae sink to deeper waters as all catches from deeper levels show. The specific gravity of empty thecae may be greater than that of the whole organism. Autotomy leaves the thicker and presumably denser parts of the theca upon the organism and in so far tends to increase its specific gravity, thus tending to sink it to lower levels or assisting it in retaining its position at a certain distance *below* the surface when temperatures are lowered.

More patent still is the change in *specific surface* which must result from autotomy. This removes from the body the slender horns, those parts in which the number of units of surface to each unit of volume is greatest. By the process of autotomy the volume of the organism is reduced, but proportionately less than its surface. This results in a decrease in the specific surface and

therefore of the resistance which the molecular friction of the water affords to the sinking of the body.

Ostwald (:03) has defined specific surface as the ratio of absolute surface to absolute volume. Computation of the actual surface and volume of a normal individual of *C. gallicum* and of the horns beyond a plane of autotomy midway in their length gives the following results, when S and V represent respectively the surface and volume before autotomy and s and v the corresponding measurements of the horns beyond the plane of section.

$$\frac{S}{V} > \frac{S-s}{V-v} \text{ or } 265 > 210.5.$$

The decline in specific surface is thus about 20.5%. Applying this to Ostwald's (:03) computations of the changes in molecular friction attendant upon changes in temperature we find that an increase of 20.5% in the molecular friction found in sea water at 20% would be equivalent to a drop in temperature of 7.43°. In other words, a normal *C. gallicum* before autotomy floating in water at 20°, would, other things being equal, be equally adapted to flotation in water at 12.57° by the autotomy of its horns midway in their length. Without autotomy its specific surface upon the lowering of the temperature would be in excess of its needs and would tend to maintain the organism in levels nearer the surface when once it entered them.

The cause of autotomy is not easily determined in view of the complex and largely unknown chemical and physical factors involved. Nevertheless the data of its occurrence are suggestive of the agency of certain of these factors, which may, moreover, be tested by experiment. *Ceratium* presents in its structure certain conditions peculiar among unicellular organisms, namely that of three distally projected protoplasmic horns which secrete upon their surface a continuation of the cellulose wall of the mid-body. The synthetic processes of the cell go on only in the presence of the nucleus. The distance from the nucleus at which the metabolic processes involved in the secretion of cellulose can go on are possibly affected by temperature. Whether or not this results from the relation of temperature to the velocity of chemical reactions, we do not know. The facts are that in warmer waters the horns of practically all species are projected to a pro-

portionately greater distance from the nucleus than they are in colder waters. The contrast in length of horns of *Ceratium* from tropical and arctic waters has been a matter of frequent comment (see Chun '02) and the principle of the correlation of the processes of pelagic organisms with the function of flotation has often been noted [see Wesenberg-Lund (:00) and Ostwald (:03)]. Temperature thus bears a definite relation to the distance from the nucleus to which the horns of *Ceratium* may extend. In high temperatures this distance is greater than at low ones. So also

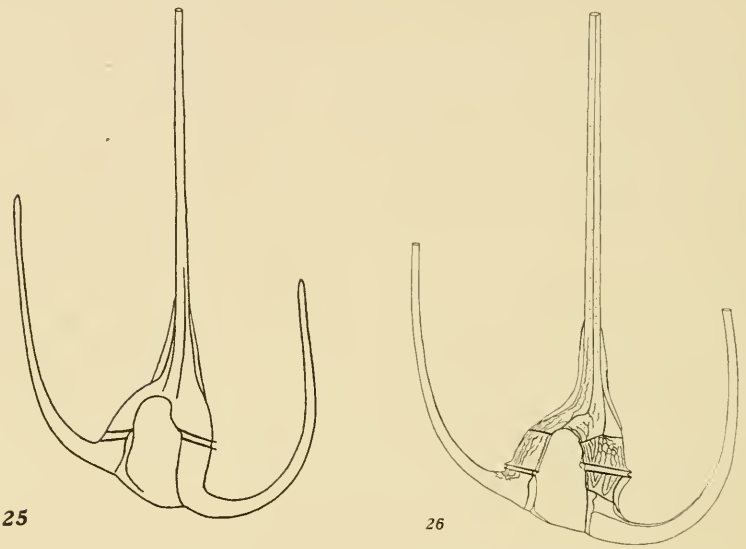


Fig. 25.—Ventral view of a normal *Ceratium arcuatum*. × 155.

Fig. 26.—Ventral view of another individual after distal autotomy of the tips of the antapicals. × 160.

in the fully grown organism it may follow that the distance in the horn to which the normal processes of metabolism can be maintained is in a similar manner affected by temperature. A long-horned *Ceratium* entering a region of cooler water suffers, it may be, a reduction in the radius of action of nuclear activity and autotomy of a regulatory character follows. The suggestion naturally arises that under conditions of lowered temperature a ferment is produced or becomes effective which brings about a resolution of the wall and that the temperature regulates

the distance from the nucleus at which this reversal of the secretion process to one of resolution takes place. A suggestive parallel to this phenomenon is seen in the reversal of heliotropism of pelagic organisms by change in temperature described by Loeb ('93).

III. Regeneration in Ceratium.

1. *After schizogony.* In normal schizogony the naked portion of each segment is immediately covered by a duplication of that part of the ancestral thecal wall passed to its sister schizont.

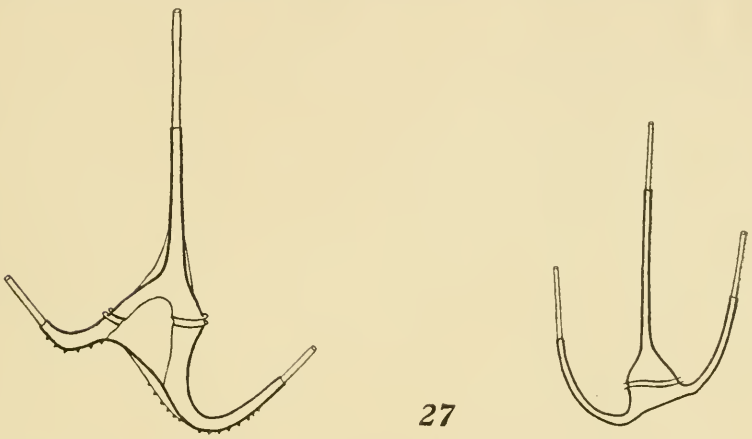


Fig. 27.—Ventral view of *Ceratium ostenfeldi* (?) and dorsal of *C. intermedium* showing proportional regeneration of all three horns presumably after autotomy. × 155.

When it first appears this newly formed wall is an exceedingly thin, structureless film which, by a process of thickening and superficial differentiation, rapidly takes on a facies similar to that of the inherited part of the theca. In all essential particulars this process is similar to the form regulation that attends the fission of other protozoa or of a planarian, but, owing to the considerable differentiation of the skeletal parts and the retention of half the ancestral skeleton, the resemblance to the process of regeneration of lost parts is the more striking.

2. *Regeneration after autotomy, or independently of it.* Autotomy is accompanied in this genus by the capacity for re-

generation of the horns. *Ceratium* exhibits, however, the capacity of increasing the length of its horns quite apart from autotomy. In species of the *C. macroceros* group in which the antapical horns have open tips the horns increase in length by simple extension of the protoplasm and its accompanying wall. In

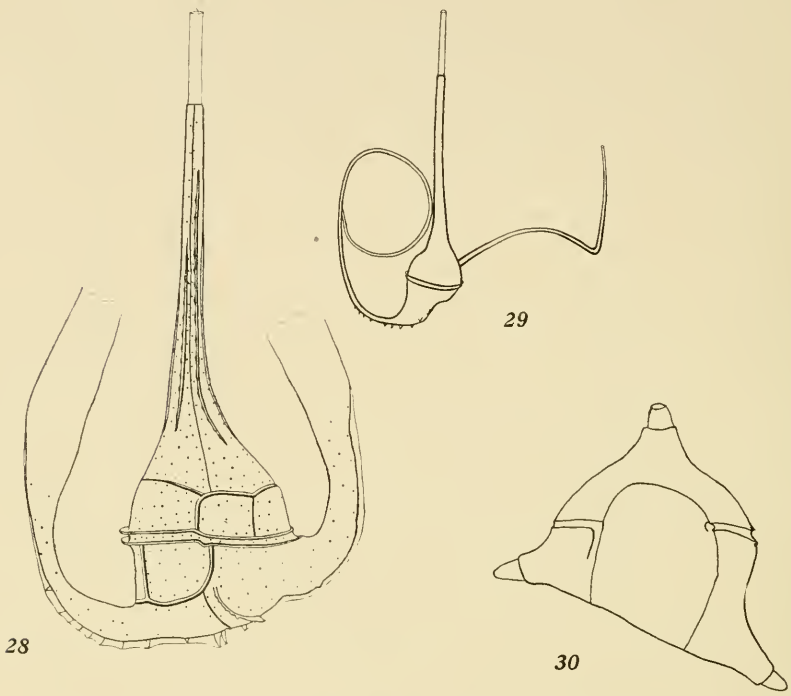


Fig. 28.—Dorsal view of *Ceratium lamellicorne* (nomen novum = *C. tripos* forma *dilatata* Karsten = *C. ditatatum* (Karsten) Kofoid) showing renewed growth of the apical horns. × 440.

Fig. 29.—Dorso-lateral view of *Ceratium reticulatum spirale* showing the same. × 100.

Fig. 30.—Ventral view of *Ceratium divaricatum,* showing regeneration of all three horns after basal autotomy. × 100.

figure 27 are shown individuals of *C. intermedium* and *C. ostenfeldi* (?), in which all these horns are thus being extended apparently after autotomy, for, with this extension the total length is still within the norm of the species. The regenerated parts are exceedingly thin-walled and have apparently just formed and not

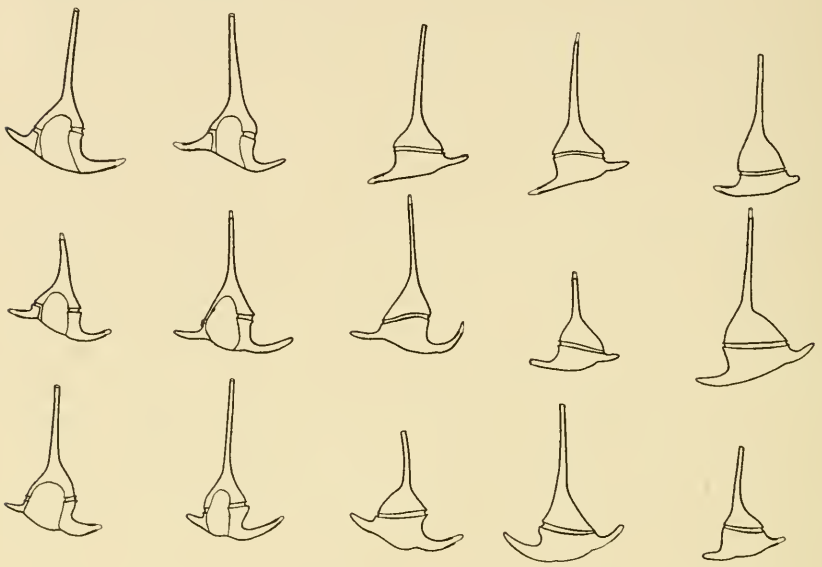
yet attained the length, thickness or surface markings characteristic of the species. This growth is apparently not a prolonged process, but one abruptly made, in like manner to the original growth of the horns. The evidence for this lies in the fact that the newly found portions of the wall are of approximately uniform texture throughout their length. They are also formed coincidently, since they are of similar texture on the three horns. Observations on many instances of regeneration in many species of *Ceratium* bear out the statement here made concerning their rapid and coincident formation. In figures 28 and 29 are shown similar instances of distal regeneration of the apical horn in *C. lamellicorne* and *C. reticulatum spirale.*

Regeneration proceeds in a slight measure, however, centrifugally from the stump of the horn. This is seen in the fact that occasionally individuals are found in which the protoplasm is naked distally or in which the distal part of the newly formed section of the horn is more delicate than the proximal. Such differences are, however, relatively insignificant and temporary.

3. *Regenerative growth independent of autotomy.*—In species having antapicals with closed tips such as those of the *C. tripos* and *C. furca* group I have found some evidence of distal extension of the antapical horns without preceding autotomy. In figure 26 is seen an individual of *C. arcuatum* which has undergone distal autotomy, and in figure 25 an instance of distal regeneration of the closed tips, apparently after autotomy. In the course of my examination of collections I have found numerous cases of subsequent distal regeneration of new tips after such distal autotomy in various species of the *C. tripos* group.

In a plankton collection taken July 12, 1904, in a haul from 75 fathoms to the surface there were a large number of *Ceratium divaricatum* in which there was renewed centrifugal growth at the *tips* of the closed antapicals and occasionally also of the tip of the apical as shown in figure 31. In some cases all three horns had renewed distal centrifugal growth, in others only the apical, and in still others either one or both of the antapicals. In no observed case, however, does the growth reach an extent which carries any of the horns beyond the normal range of variation in this species. This growth in *C. divaricatum* takes place at the

opposite end of the horn from that noted below in *C. californiense.* The prevalence of this renewed growth on the otherwise rugose thecae of the former species is strongly suggestive of a general readjustment of specific surface in this instance by prolongation of the horns brought about by growth of the regenerative type. In figure 30 is shown an instance of regeneration of all three horns *after autotomy* which left little of the organism save the midbody.



31

Fig. 31.—Examples of regenerative growth in distal locations on the horns of *Ceratium divaricatum.* All from the same plankton collection. × 100.

In *C. californiense* (figs. 31 and 32) I have found one instance of *proximal growth in the antapicals without preceding autotomy.* In this species the tips are closed and the zones of new growth are at the *bases* of the antapical horns and the old thick-walled antapicals are carried out distally on the intercalated new zone. The apical horn on the other hand has a *distal zone* of new growth of a length corresponding to that which has taken place at the bases of the other two horns. It is obvious that this instance is not one of typical regeneration, for no parts

were lost prior to the renewed growth. The process and the function served are, however, in many aspects similar to those in typical regeneration.

4. *Regulatory nature of regeneration of the horns.*—In both of these types of regeneration or new formation of the horns, the extensions of the horns exhibit the same kind of form regulation as that which appears in normal growth. The proportions characteristic of the species are maintained by the coincident extension of both antapicals and of the apical also, in case it is proportionately short at the time of regeneration.

The regulatory character of the regeneration of the horns after autotomy and independently of it is evident on inspection of the table on p. 368. In nine of the fourteen cases of regeneration all three horns regenerate together. The apical does not exhibit this phenomenon in five instances and shows less growth than the antapicals in all but three cases. In three of the fourteen instances of regeneration the growth of the right horn exceeds that of the left, in three cases it equals it, while in the remaining eight it shows less growth. It appears that the same causes which control the extension of the horns in normal growth are operative in the majority of instances to control their extension in regeneration.

5. *Significance of regeneration.*—It is obvious that increase in the length of the horns, of those parts of the body in which the number of units of surface per unit of volume, is greatest, results in a relative increase of surface and a rise in the specific surface of the organism. Increased specific surface is an adaptation of flotation in water of higher temperature. Individuals in which these extensions have occurred will be able to maintain their customary location in the face of a rise in temperature up to a certain point, or to retain their position at given levels in warmer waters into which they might move. The extent to which these distal growths of the horns may be operative in adjustments of capacity for flotation may be illustrated in the case of *C. californiense*.

This specimen with renewed growth (figs. 32 and 33) was taken May 28, 1904, 10 miles west of Pt. Loma over Cabral's Banks in a haul from 75 fathoms. Surface waters on that day

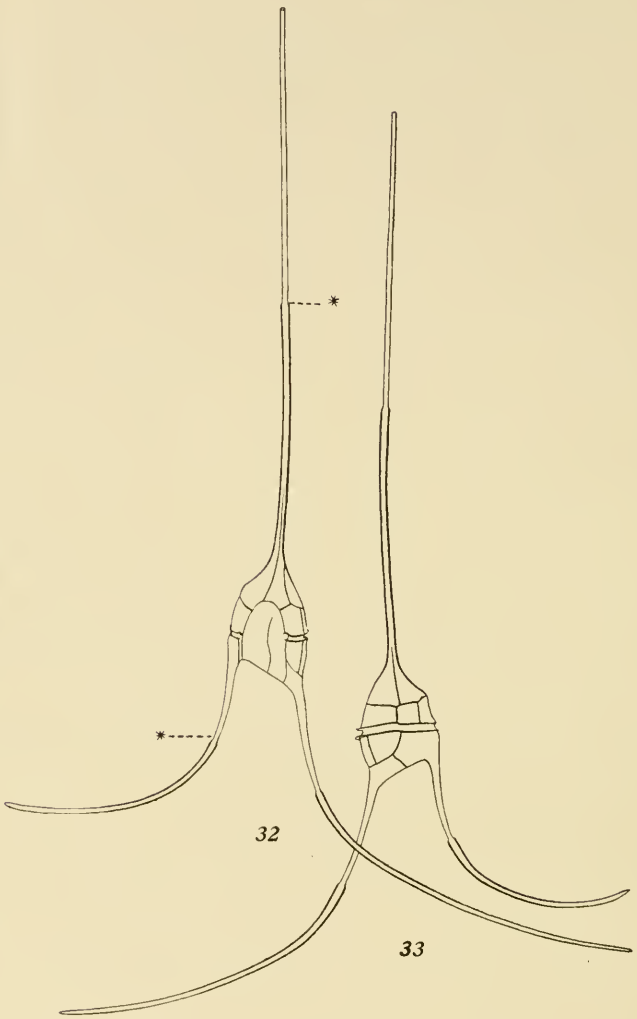


Fig. 32.—Ventral view of *Ceratium californiense* showing regenerative growth at the distal end of the apical and proximal ends of the antapical horns. Points of junction of new and old growth marked by an asterisk. × 300.

Fig. 33.—Dorsal view of the same. × 300.

off Coronado Pier had a temperature of 20.8°. Temperature of water off San Diego pumped from a depth of 70 fathoms on June 30, 1903, was 14.2°, on July 1 was 14.7°, on July 2 from 72 fathoms, was 15°, on July 3 from 70 fathoms, was 14.7°, on July 7 from 72 fathoms was 15°, and on July 9 from 72 fathoms was 15.5°. It is possible that the extreme limits from which this particular specimen might have been taken lie approximately between about 14° and 20.8°. If it had taken on its new growth to adjust its flotation in water which had risen to 20.8°, the 19% increase in specific surface would, according to Ostwald's (:03, p. 62) table of temperatures and molecular friction, accommodate the organism to an advance from 12.25° to 20.8°, or to a rise of 8.55°. Tests of vertical distribution of temperature made off San Clemente Island in July, 1905, with the self-closing water bottle (see Kofoid :05) indicate that a decline of temperature to this extent occurs within approximately 200 fathoms of the surface. This distance, 200 fathoms to the surface, is quite within the range of the possible distribution of this organism. This is a somewhat close approximation between the increase in specific surface caused by the renewed growth and the changes in molecular friction due to the range of temperatures in the possible habitat of the species. This close agreement between Ostwald's experimental determinations and my computations of the changes in specific surface of this pelagic organisms are all the more striking and significant if the probability of error in the determination of the specific surface of so small and irregular a body as that of *C. californiense* is borne in mind and also the certainty that other factors enter to modify the process of adjustment, such as alterations in specific gravity which might follow from changed proportions of thin and thick thecal wall, and from modifications in metabolism and in cell contents attendant upon increased illumination and reduced pressure.

Summary.

In some Dinoflagellata ecdysis, or the shedding of the total exoskeleton does not occur.

In those genera, such as *Ceratium*, in which the theca is shared between the daughter schizonts at schizogony, compensatory re-

generation of the newly forming part of the exoskeleton occurs. Skeletons of senile facies may be removed by exuviation, plate by plate, often at the time of schizogony. This exuviation makes possible readjustments of specific gravity and specific surface to changing conditions of flotation.

Autotomy of the two antapicals, or of all three horns is of widespread occurrence among many species of Ceratium. It is more abundant in collections from deeper levels than in those from the surface. It is caused by local resolution of the cellulose wall and is regulatory in character, preserving in the horns after autotomy the proportions characteristic of the species. Autotomy assists in the adjustment of specific surface and possibly also of specific gravity to changing conditions of flotation, especially as affected by temperature.

Regeneration of the horns with or without preceding autotomy may occur in all three horns. It is also regulatory in character and tends to preserve the norm of the species.

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CONTRIBUTIONS FROM THE LABORATORY
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MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO.

XXII.

NOTES ON SOME OBSCURE SPECIES OF *CERATIUM*.

BY

CHARLES ATWOOD KOFOID.

The publication of the preceding paper (Kofoid ('08)) has necessitated the recognition of certain species in the genus *Ceratium* which either have not appeared in the current literature dealing with this polymorphic genus, or if they have been cited, the nomenclature used requires revision.

In 1874 Ehrenberg, in a paper published in the centennial volume of the "Gesellschaft für Naturforschenden Freunden zu Berlin" under the title "Die das Funkeln und Aufblitzen des Mittelmeeres bewirkenden unsichtbar kleinen Lebensformen" figured and described briefly several species of *Ceratium* which seem to have been overlooked generally by subsequent investigators. Ehrenberg's paper has escaped the notice of later monographers, even of Bütschli ('83-'87) and of Schütt ('95 and '96), for neither lists it in his bibliography of the *Dinoflagellata*.

Among other organisms of the plankton this paper describes four species of *Ceratium* as of the genus *Peridinium*, to wit: *P. Trichoceros*, *P. Candelabrum*, *P. cugrammum*, and *P. Seta*. Of these *P. candelabrum* was later recognized by Stein ('83), who, however, reduced *P. trichoceros* to a synonym of *C. tripos*,

and *P. Seta*, to a synonym of *C. fusus*, in the explanation of his Tafel 16, while *P. eugrammum* is referred to *C. furca*, in the explanation of his Tafel 15.

It is not improbable that the reduction of these species of Ehrenberg's to synonyms by Stein ('83) is due to Stein's knowledge only of an earlier paper of Ehrenberg's ('60) in which he briefly diagnosed these species, but without figures, in the absence of which their recognition is difficult, if not impossible. Later authors have, with the exception of Saville-Kent ('81-'82), concurred in Stein's opinion.

I have elsewhere (:07) noted the correctness of Ehrenberg's recognition of *C. eugrammum*. I wish here to revive two of his other species of *Ceratium*, which are equally valid, and to note the instances in which several of them have crept into literature under new names in recent years.

Ceratium trichoceros (Ehrbg.).

Ehrenberg ('60), p. 791, as *Peridinium Trichoceros.*
Ehrenberg ('74), p. 3, Taf. (1), fig. 1, as *Peridinium Trichoceros.*
Saville-Kent ('80-'81), vol. 1, p. 457, as *Ceratium seta.*
Stein ('83), explanation of Taf. 16, as a synonym of *C. tripos.*
Karsten (:06), Taf. 22, fig. 31b, as *C. flagelliferum* Cleve; fig. 32a and b, as *C. flagelliferum* forma *crassa* n. var. The latter figure is questionably referred to *C. trichoceros* by me.
Kofoid (:08), p. 362, figs. 15-19.

This species of Ehrenberg's is well defined by its rigid habit of growth, the wide-spreading major flexures of the antapicals, and the slender horns with pointed closed tips. Its three horns are subparallel and the antapicals are usually noticeably serrate along their posterior margin toward their major flexures.

It has probably been confused in the past with *C. flagelliferum* Cleve (:00), a form of *C. inflexum* Gourret ('83), which has more flexible or variously incurved or recurved antapicals and exhibits in general a more lax habit of growth than *C. trichoceros*. The tips of the antapicals of *C. inflexum* are contracted, usually have a small terminal pore and are sometimes swollen, differing in these particulars from the pointed closed tips of *C. trichoceros*. *C. inflexum* also lacks, as a rule, the prominent posterior serrations of *C. trichoceros*.

Ceratium seta (Ehrbg.).

Ehrenberg ('60), p. 792, as *Peridinium Seta.*
Ehrenberg ('74), p. 3, Taf. (1), fig. 1, as *Peridinium Seta.*
Saville-Kent ('80-'81), p. 457, as *Ceratium seta.*
Stein ('83), explanation of Taf. 15, as a synonym of *C. fusus.*

A careful examination of the species of the *Ceratium fusus* group which I have recently made at San Diego convinces me that Ehrenberg was correct in distinguishing *C. seta* as a species distinct from *C. fusus.*

Ceratium seta has a less broadly fusiform midbody, its transdiameter averaging 10 μ less than that of *C. fusus.* Its surface is less rugose, its curvature usually more pronounced, and its right antapical uniformly suppressed, whereas this horn is short but uniformly present in *C. fusus.* Another striking difference lies in the fact that the hypotheca exceeds the epitheca in the former species, but these relations are reversed in *C. fusus.*

Gourret ('83) describes, as *C. fusus* var. *extensum* and *C. longirostrum,* certain long-horned forms resembling *C. seta.* A statistical study of material from the oceanic plankton off San Diego leads me to regard these as forms of one species, *C. extensum* (Gourret), which, however, is distinct from *C. seta.*

Ceratium biceps Clap. et Lachm.

Claparède et Lachmann ('58-'59), pp. 400-401, pl. 19, fig. 8.
Gourret ('83), pp. 55-56, pl. 1, fig. 19, as *C. Berghii.* Symmetry reversed in figure.
Okamura and Nishikawa (:04), p. 128, pl. 6, fig. 25, as *C. fusus* var. *stricta* nov. var. prov.
Kofoid (:07), p. 133, as *C. strictum.*
Kofoid ('08), p. '00, figs. 21-24, as *C. biceps.*

In my opinion Claparède and Lachmann described as *C. biceps* an individual which had recently undergone autotomy and had in consequence relatively short apical and left antapical horns. Their figure will bear the closest comparison with such mutilated specimens. Later Gourret ('83) gives a reversed figure which may be referred provisionally to this species. Okamura and Nishikawa (:04) were the first to publish a typical figure showing the normally developed horns, but they did not recognize the similarity of the species with which they were dealing to that

previously described by Claparède and Lachmann, or Gourret; nor did they call attention to the short forms of this species which result from autotomy. When this phenomenon of autotomy is borne in mind we may utilize Claparède's and Lachmann's description and revive their name for this well defined species.

Ceratium biceps is a large species differing from *C. fusus*, and *C. seta* in its greater length, and from *C. extensum* in the presence, uniformly, of a right antapical horn or its truncated stump, in its larger midbody and in the less curved, slightly deflected, left antapical horn.

Ceratium lamellicorne nom. nov.

Karsten (:05), p. 132, Taf. 19, figs. 9, 10, as *C. tripos* forma *dilatata*.

Kofoid (:07), p. 171, pl. 4, fig. 25, as *C. dilatata* (Karsten).

Karsten (:07a), Taf. 48 (14), figs. 10a, 10b, as *C. tripos platycorne* Daday. Karsten's Taf. 51, figs. 4a, 4b, also called by him *C. tripos platycorne* Daday, is the typical *C. platycorne*.

Kofoid (:08), p. 185, fig. 28, as *C. lamellicorne*.

This is a small species of the *C. platycorne* group, with the antapicals expanded into a thin sheet in the plane of the three horns. It differs from the true *C. platycorne* in its smaller size and relatively shorter antapicals which are also narrower with a more regular curvature and a more uniform width throughout their length. They lack the characteristic swelling found on the median margin of the antapicals of *C. platycorne*. Karsten's earlier figures (:05), designated by him as *C. tripos* forma *dilatata*, are in my opinion *C. lamellicorne*. His later figures (:07) are in part (Taf. 48, figs. 10a, 10b), of the *C. lamellicorne* type and in part (Taf. 51, figs. 4a, 4b) of the type originally described by Daday ('88) as *C. platycornis*. On the grounds above stated I regard the two species as distinct.

In his earlier paper Karsten (:05) makes no mention of the species described by Daday and we are left without any evidence in his brief descriptive text as to whether or not he regarded the two forms as distinct. In his later paper (:07, p. 406) he discusses the question and concludes that his forma *dilatata* is only a young form of *C. platycorne*, in which the antapicals have not

as yet expanded to the size that they later attain in the older stage.

As above stated, *C. lamellicorne* is smaller than *C. platycorne*. This applies to the length of the horns, which, as I have shown in the preceding paper, might be expected to undergo changes in length during the life of the individual by processes of autotomy, regeneration, or growth of regenerative type. Lateral expansion of the median margin of the antapical horns is also theoretically possible. The midbody, however, is typically larger in *C. platycorne* than in *C. lamellicorne*. I have no evidence that the midbody of *Ceratium* is subject to an increase in size comparable with that which may occur in the horns.

A consideration of the conditions pertaining to the skeleton during schizogony, especially the fact of compensatory regeneration of the new skeletal moiety, and the essential uniformity of individuals in chain, would seem to preclude the existence of any such young and old stages of the individual with accompanying differences in dimensions due to growth, such as would necessarily follow from Karsten's point of view with regard to these two forms. I find no such prevalence of intergrades as the idea that *C. platycorne* is the old stage of *C. lamellicorne* would lead us to expect. An examination of a large number of sketches of these two species of *Ceratium* from the oceanic plankton off San Diego leads me to believe them to be distinct species with a constant size difference and not age forms of one.

Karsten's (:05) name *dilatata* is preoccupied by Gourret's ('83) *C. dilatatum*. Gourret seems also not to have known of Ehrenberg's ('74) description of *C. candelabrum* and among other names which he has applied to various forms of that polymorphic species, he uses *C. dilatatum*. Because of Gourret's prior use of this name I here propose for this smaller species the new name of *C. lamellicorne*.

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April 2, 1908.

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INDEX.*

Synonyms are in *italics;* names of **new species**, etc., and titles of papers, are in **bold-face.**

Abyssal Styelas, 22.
Abyssascidia, 28, 29, 30.
Affinities, of Benthascidia, 29.
Agnesia, 29, 30.
Alaskan waters, 13, 23.
Albatross, United States Fisheries Bureau Steamer, 1.
Amphiflustrum bitubereulatum, 265.
Allman, J. G., cited, 316.
Amphioxus, 202, 203; compared with Dolichoglossus pusillus, 213; origin of mesoderm in, 213-4.
Annelids, cleavage of egg in, 204.
Arctic regions, 13.
Arnold, R., cited, 316.
Ascidia clementea, n. sp., 2.
Ascidia, 34; cleavage of, compared with Dolichoglossus and Amphioxus, 203.
Ascidians, the, collected by the United States Fisheries Bureau Steamer Albatross, 1.
—bathymetric distribution of, 2.
Ascidiella, 34.
obliqua, 35.
Ascidiidae, 2.
Assimilative regeneration, 363.
Asterias, behavior of, 53.
Asterias glacialis, pedicellariae in, 63.
Astropera, 8.
Atrial orifice in Benthascidia, 25.
Autotomy in Ceratium, 360; general occurrence, 361; frequency in collections from deep water, 363; evidence of, 363; regulatory character of, 364; significance of, 374; relation to specific gravity, 374; to specific surface, 374.
Balanoglossus, 213-4.
kowalevskii, period of larval development, 190; mesoblast of, 210.
Bateson, W., cited, 188, 209-10-11-12.
Bathyoncus, 29, 30.
Bathypera, 29, 30.
splendens, 29.
Behavior, the, of the Starfish Asterias Forreri de Loriol, 53.
Benthascidia, n. gen., 2, 23; affinities of, 29; atrial orifice in, 24; brachial sac of, 23, 28; dorsal languets of, 27; dorsal tubercle of, 27; endostyle of, 28; holdfasts of tentacles, 27; n. gen., 23; pedunele of, 26.
Benthascidia michaelseni, n. sp., 2, 24, 29.
Berenicia, 301.
(part) Fleming, 307.
Bering sea, 13.
Bibliographies, 45, 184, 216, 242, 316, 385, 392.
Biflustra denticulata, 265.
laeroixii, 261.
tehueleha, 265.
Blainville, H. M. de, cited, 316.
Blastopore, 206, 211.
Body cavities, middle and posterior of Dolichoglossus pusillus, 208, 211; comparison with amphioxus, 213; homology of, 215.
Boltenia bouvetensis, 16.
echinata, n. sp., 2, 14, 15.
elegans, 16.
Bowers, G. M., acknowledgment to, 239.
Bradley, J. C., 227.
Branchial sac of Benthascidia, 28.
Bryozoa, list of species treated, 254.
Burrow of Dolichoglossus pusillus, 189, 195, 198.
Bütschli, O., cited, 387.
Calcareous spicules, 3, 4, 7.
Castle, W. E., cited, 201.
Cellepora, 257.

* Univ. Calif. Publ. Zool., vol. 4.

Cellepora costazi, 313.
(part) Fabricius, 312.
(Fleming), 300.
Hincks, 312.
hyalina, 289.
incrassata, 312.
malusii, 282.
Celleporidae, 256.
Hincks, 312,
Cell wall, structure of, 349.
Ceratium, regeneration after autotomy, 377; after schizogony, 377; autotomy in, 360; evidences of, 363; frequency in collections from deep water, 363; general occurrence, 361; regeneration independent of autotomy, 379; regeneration in, 377; regulatory nature of, 381; relation of autotomy to specific gravity, 374; to specific surface, 374; senile forms in, 355; significance of autotomy in, 374; summary, 383.
Ceratium arcuatum, 376, fig. 25.
arcuatum (?), 357, fig. 11.
biceps, 371, figs. 21-3, 389, 390.
californiense, 382, fig. 32.
divaricatum, 378, fig. 30, 380, fig. 31.
eugrammum, 350, fig. 5.
gallicum, 361, figs. 13-15.
intermedium, 377.
lamellicorne, 378, fig. 28, 390.
ostenfeldi (?), 377, fig. 27.
protuberans, 354, fig. 10, 363, fig. 20.
reticulatum spirale, 378, fig. 29.
seta, 389.
trichoceros, 362, figs. 16-19, 388.
vultur, 352, fig. 9.
Cerfontaine, P., cited, 214.
Challenger, 23.
Chilostomata, 255; incrusting, key to families of, 256.
Cilia, of Tornaria, 194.
Ciona, viscera in, 39.
Ciona intestinalis (Ascidia), comparison with Dolichoglossus pusillus in early cleavage, 203.
mollis, n. sp., 2, 35, 39.
savignyi, 39.
Clavelina, 29, 30.
Cleavage of ascidian egg, 204; of Dolichoglossus pusillus egg, 201-5; of mollusks, 204.
Cleve, P. T., cited, 388.
Climacteric period in larval life of Enteropneusta, 190.
Cole, L. J., cited, 111.
Conklin, E. G., cited, 201.
Corella, 28.
Corophium, comparison of the species, 239; antennae, 240; coloration, 239; key to species of, 229; maxillae, peraeopods, 240; uropods, 240.
Corophium acheruzicum, 230.
affine, 230.
bonelli, 230.
chelicorne, 229.
crassicorne, 230.
curvispinus, 230.
cylindricum, 230.
maeoticum, 229.
monodon, 230.
mucronatum, 230.
nobile, 230.
robustum, 230.
runcicorne, 230.
salmonis, antennae, 235; gnathopods, 236; maxillae, 236; maxillipedes, 236; original description of, 229; peraeopods, 237; plate 11, 12, 13; uropods, 238.
spinicorne, antennae, 230; gnathopods, 232; maxillae, 232; paraeopods, 233; plate 9, 10, 13; uropods, 234.
spinulosum, 229.
triaenonyx, 229.
volutator, 229.
Corynascidia, 27, 28, 29, 30.
Crabs, capture of by starfish, 85.
Cribrilina, 279.
Cribrilina annulata, 280.
hippocrepis, 254, 280.
Cribrilinidae, 256, 279.
Cuenot, L., cited, 65.
Culeolus, 18, 22.
murrayi, 18.
pyramidalis, n. sp., 2, 16, 18.
quadrula, 17.
thysonatus, 18.
Cupularia, 314.
Cupularia canariensis, 314.
Cupulifera, 314.
Cynthia, 35.
Cynthiidae, 2.
Cyphonautes, 257-8, 271.
Cyphonautes compressus, 272.
occidentalis, 254, 272.
Cystodites cretaceous, 2, 39.
cretaceous (?), 39.
Delle Chiajae, 40.
Cytecdysis, 347.
Daday, E. C., cited, 390.

Davis, B. M., 187.
Deep-sea genera, 22.
Deep water, collections from, 363.
Della Valle, A., cited, 228, 242.
Development, direct, of Enteropneusta, 188; of Tornaria, 190; larval period of, 190.
Diazeuzia hyalina, 289.
retieulans, 289.
Didemnidae, 2.
Didemnum cereum, 44.
opacum, n. sp., 2, 42.
sargassicola, 44.
Dinoflagellata, ecdysis in, 347.
Diplopsalis lenticula, 348, fig. 3.
Discopora, 275, 307.
Discopora coriacea, 275.
pavonella, 308.
Distomidae, 2.
Distribution, bathymetric, of ascidians, 2; of Dolichoglossus pusillus, 195-6-7.
Dolichoglossus kowalevskii, mesoblast of, 210.
Dolichoglossus pusillus, blastopore of, 206; burrow of, 189, 195, 198; compared with amphyoxus, 213; distribution of, 195; early growth, stages of, 200; eggs of, 189; egg cleavage of, 201-5; embryos, half and double, 213; gastrula of, 204; gill openings of, 205-6; habits and activities of, 192; homology of, 215; larval life of, 190; material and methods of study, 188; mesoderm and body cavities of, 207-9; specific gravity of, 198.
Donati, V., cited, 317.
Drasche, 40.
Driesch, H., cited, 58, 122, 153; doctrine of entelechy, 174.
Early Life-History, the, of Dolichoglossus pusillus Ritter, 187.
Ecdysis, occurrence in dinoflagellata, 347; relation to schizogony, 348.
Ectoprocta, 255.
Eggs of Dolichoglossus pusillus, 189.
Embryos, double and half, of Dolichoglossus pusillus, 213.
Ehrenberg, C. G., cited, 317, 388.
Ellis, J., cited, 317.
Endostyle, of Benthascidia, 28.
Entelechy, Driesch's doctrine of, 122, 174.
Enteropneusta, development of, 188; gland cells of, 212; larva of, 190.
Eschara, 257, 281.
Eschara biaperta, 287.
cribraria, 308.
landsborovii, 305.
pavonella, 308.
Escharella, 301.
Escharella jacotini, 302.
landsborovii, 305.
linearis, forma *biaperta*, 287.
Escharidae, 256, 297; key to genera of, 297.
Escharina personata, 289.
Escharipora, 279.
Escharoides, 298, 301.
Escharoides sarsii, 301.
Escharopsis lobata, 301.
Eugyra molguloides, 7, 8.
Eupera, 29, 30.
Exuviation, Autotomy and Regeneration in Ceratium, 345.
Exuviation, 349.
Fabricius, O., cited, 317.
Fleming, J., cited, 317.
Flotation, 81, 376.
Flustra, 275.
Flustra cecilii, 288.
coriacae, 275.
distans, 261.
isabelliana, 269.
lacroixii, 261.
lineata, 265.
rozierii, 277.
spinifera, 265.
tehuelcha, 265.
Gastrula, of Dolichoglossus pusillus, 204, 206.
Genera, deep-sea, 22; of escharidae, 297.
Gill openings of Dolichoglossus pusillus, 205.
Gland cells of enteropneusta, 212.
Glaser, O. C., cited, 153.
Gonyaulax polyhedra, 347.
Gourret, P., cited, 388-9.
Growth, stages of, of Dolichoglossus pusillus, 200.
Gymnolaemata, 255.
Habits and activities of Dolichoglossus pusillus, 192.
Habits in the starfish, 148.
Haloeynthia, 15.
Haloeynthia aretica, 13.
castaneiformis, 13.
echinata, 12.
hilgendorfi, 12, 13.

okai, n. sp., 2, 3, 11, 12, 15.
owstoni, 12.
ritteri, 12.
villosa, 12.
Halomolgula, n. gen., 1.
Halomolgula ovoidia, n. sp., 1, 3, 8.
Hartmeyer, R., cited, 10.
Herdman, W. A., cited, 23, 27, 31, 37.
Hippothoa biaperta, 287.
divaricata, 296.
divergens, 287.
Hold-fasts of Benthascidia, 26.
Holway, R. S., 363.
Hypobythius, 28, 29, 30.
Incrusting Chilostomatous Bryozoa of the West Coast of North America, 253.
Infundibula in Molgula ovoidia, 6.
Intelligence of starfish, 152.
Japan, 13.
Jennings, H. S., 53.
Karsten, G., cited, 390.
Kiaer, J., cited, 11, 35.
Kofoid, Charles Atwood, 228, cited; 345, 387.
Lagenipora, 283.
Lagenipora spinulosa, 254, 283.
Lahille, F., cited, 44.
Languets, dorsal, of Benthascidia, 27.
Larva of enteropneusta, 190.
Lauterborn, R., cited, 352.
Lepralia, 279, 298; (Busk) 300, 301; (Johnston) 279, 281, 285, 298, 301, 307.
Lepralia areolata, 285.
auriculata, 286.
biaperta, 287.
bilabiata, 298.
californica, 281.
cecilii, 288.
concinna, 300.
discreta, 289.
hyalina, 289.
landsborovii, 305.
linearis, 291.
var. *biaperta*, 287.
malusii, 282.
ochracea, 286.
perugiana, 288.
reticulata, 305-6.
trispinosa, 302.
variolosa, 302.
Light, reaction of starfish to, 102.
Lobes, secondary, of the papillae in Ciona mollis, 38.
Loeb, J., cited, 58, 97, 121, 377.
Magellan, straits of, 22.
Mediterranean, 40.
Membranipora, 257, 275; key to species of, 258.
Membranipora californiensis, 260.
canariensis, 314.
cellepora, 257.
circumclathrata, 258-9.
cymbaeformis, 265.
gothica, 277.
horrida, 258, 260.
lacroixi, 258, 261.
membranacea, 258, 267.
form *serrata*, 268.
occultata, n. sp., 258, 262.
patula, 258, 263.
sandalia, 258, 264.
serrata, 258, 268.
spinifera, 258, 265.
tehuelcha, 258, 265.
tuberculata, 265.
unicornis, 262.
villosa, 258, 269.
Membraniporae, metamorphosis of, 272.
Membraniporidae, 256.
Mesoblast of Dolichoglossus kowalevskii, 210.
Mesoderm of Dolichoglossus pusillus, 207.
Metamorphic period in larval life of enteropneusta, 190.
Metamorphosis of membraniporae, 272.
Michaelsen, W., cited, 16, 22, 29, 31; species dedicated, 32.
Microcosmus, 35.
Microcosmus arenaceous, 20.
transversus, n. sp., 2, 18, 20.
Micropora, 275.
Micropora coriacea, 254, 275.
ciliata form californica, 281.
Microporella, 281.
Microporella californica, 254, 281.
malusi, 254, 282.
Microporellidae, 256, 280.
Microporidae, 256, 275.
Millepora, 294, 309, 312.
Molecular friction, 360.
Molgula arctica, 10.
ovoidia, infundibula in, 6.
regularis, n. sp., 1, 8, 10.
tenax, 10.
Molgulidae, 1, 6.
Mollia divaricata, 296.
Molluscoida, 255.
Mollusks, cleavage of egg of, 204.

Monterey Bay, 1, 39.
Monterey district, 3, 15.
Morgan, T. H., cited, 211, 212.
Mucronella, 298, 307.
Mucronella californica, sp. nov., 308.
pavonella, 308.
Myriapora, 294.
Myriozoidae, 256, 284.
Myriozoum, 294.
Myriozoum coarctatum, 295.
crustaceum, 295.
subgracile, 296.
Nathanson, A., cited, 346, 385.
Neapolitan specimens, 40.
Notes on some obscure Species of Ceratium, 387.
Notes on two Amphipods of the Genus Corophium from the Pacific Coast, 227.
Octacnemus, 26.
Oka, O., cited, 12.
Okamura, K., and Nishikawa, T., cited, 389.
Organs, renal, 5.
Orifice, atrial, in Benthascidia, 25.
Ostwald, W., cited, 346, 375.
Papillae, secondary lobes of, in Ciona mollis, 38.
Pedicellariae, 59.
Peduncle, of Benthascidia, 26.
Pera, 7.
Peridinium ovatum, 348, fig. 4.
Perophera, 38.
Phylactella, 298, 306.
Phylactella collaris, 307.
Pizon, A., cited, 8.
Point Arguello, 2.
Point Conception, 1, 2, 3.
Polyclinidae, 2.
Porella, 298, 300.
Porella concinna, 300.
Porellina, 281.
Porinidae, 256, 283.
Preyer, W., cited on the starfish, 58, 121, 150, 152.
Psammaplidium obesum, 42.
spauldingi, n. sp., 2, 41.
Reactions of starfish, 53.
Regeneration, assimilative, 353; in Ceratium, 377; after autotomy, 377; after schizogony, 377; regenerative growth independent of autotomy, 379; regulatory nature of regeneration of the horns, 381; significance of, 381.
Renal organs, 5, 6.
Reptescharella, 279.
Reptoflustra telacea, 267.
Reptoporina, 281.
Reptoporina malusii, 282.
Reptoscharella personata, 289.
Respiration in the starfish, 59.
Retepora, 298, 309.
Retepora pacifica, sp. nov., 254, 310.
pacifica catalinensis, subsp. nov., 254, 311.
Rhabdocynthia, 7, 8.
Rhizomolgula, 26.
Righting reaction of the starfish, 120.
Ritter-Davis, cited, 188.
Ritter, Wm. E., 1; cited, 13, 189.
Robertson, Alice, 253.
San Diego Bay, 197.
San Diego, Contributions from the Laboratory of the Marine Biological Association of, 53, 187, 253, 345, 387.
San Nicolas Island, 3.
Saville-Kent, W., cited, 388.
Schizogony, relation of, to ecdysis, 347.
Schizoporella, species of, 285.
Schizoporella areolata, 285.
auriculata, 285, 286.
biaperta, 285, 287.
cecili, 285, 288.
hyalina, 285, 289.
inseulpta, 285.
linearis, 254; var. inarmata, 285, 291.
longirostrata, 285, 291.
oligopus, sp. nov., 285, 292.
tumulosa, 285, 293.
Schütt, F., cited, 350, 387.
Sea-urchin, combat of, with starfish, 88.
Selenariidae, 256, 314.
Senile forms in Ceratium, 355.
Sluiter, C. Ph., cited, 8, 20, 31, 42.
Smittia, 298, 301; species of, 302.
Smittia californiensis, sp. nov., 302, 303.
collifera, sp. nov., 302, 304.
landsborovi, 302, 305.
reticulata, 302, 306.
trispinosa, 302.
Specific gravity of Dolichoglossus pusillus, 198.
Specific surface, 360, 381; relation of, to autotomy, 374.
South African coast, 42.
Spicules, 40, 42; calcareous, 3, 4, 7, 42.

Stages of early growth of Dolichoglossus pusillus, 200.
Starfish, behavior of, 53, 58; combat with sea-urchin, 88; formation of habits in, 148; intelligence of, 152; reaction of, to light, 102; respiration in, 59; righting reaction, 120; training of, 156; vision in, 110.
Stebbing, T. R. R., cited, 227-8.
Steganoporellidae, 256.
Stein, F., cited, 388.
Stimpson, W., cited, 227; original description of Corophium spinicorne, 228; original description of Corophium salmonis, 229.
Stimulus of tornaria, 199.
Styela bathybia, 22.
bythia, 22.
canopus var. magalhaensis, 22.
flava, 22.
gibbsii, 2, 23.
glans, 22.
milleri, n. sp., 2, 21, 22.
oblonga, 22.
persona, 37.
pusilla, 22.
squamosa, 22.
Styelas, abyssal, 22.
Summaries, 183, 383.
Surface, specific, reduction in, 360.
Swimming cycles of Tornaria, 193, 199.
Tadpole, gemmiparous tubes of, 43.
Tentacles of Benthascidia, 27.
Thalamoporella, 276.
rozieri, 254, 277.
Tornaria, cilia of, 194; periods of development of, 190; stimulus of, 199; swimming cycles of, 193, 199.
Training the starfish, 156.
Tubercle, dorsal, of Benthascidia, 27.
Tubes, gemmiparous, of the tadpole, 43.
Uexküll, J. V., 58, 65; on behavior of sea-urchin, cited, 74, 79, 81.
United States Bureau of Fisheries, 239.
Viscera in Ciona, 39.
Wesenberg-Lund, C., cited, 376.
Wilson, E. B., cited, 202.
Zederbauer, E., cited, 355.

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